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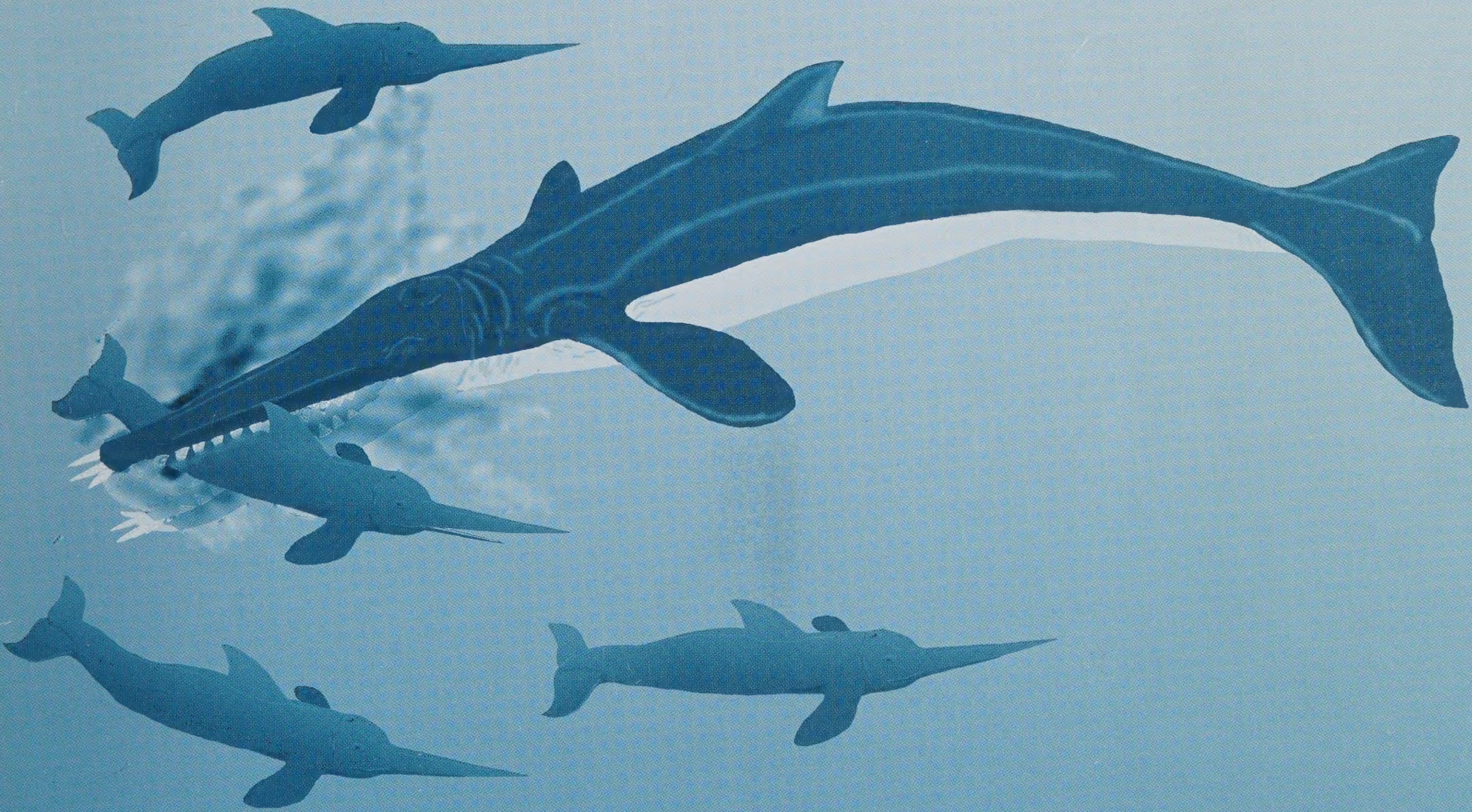
A NEW SPECIES OF *SQUALODON* (MAMMALIA, CETACEA) FROM THE MIDDLE MIOCENE OF VIRGINIA

Alton C. Dooley, Jr.



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A NEW SPECIES OF *SQUALODON* (MAMMALIA, CETACEA) FROM THE MIDDLE MIOCENE OF VIRGINIA

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Alton C. Dooley, Jr.

Virginia Museum of Natural History
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Cover image: *Squalodon whitmorei*, new species, preying on the long-beaked cetacean *Eurhinodelphis*. Drawing by Alton C. Dooley, Jr.

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TABLE OF CONTENTS

Abstract 1
Introduction 1
Materials and Methods 2
Systematic Paleontology 2
Description and Comparisons 3
    Cranium 3
    Tympanic bulla 6
    Mandible 7
    Teeth 7
    Sternum 8
    Ribs 8
    Cervical vertebrae 8
    Thoracic vertebrae 10
    Lumbar vertebrae 10
    Caudal vertebrae 10
Relationships 10
Acknowledgments 11
References Cited 12
Figures 14

A NEW SPECIES OF *SQUALODON* (MAMMALIA, CETACEA) FROM THE MIDDLE MIOCENE OF VIRGINIA

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ABSTRACT

The giant squalodontid *Squalodon whitmorei*, n. sp. is described from the Middle Miocene Calvert Formation in Virginia. The species is based on a skull, mandible, and about 70% of the postcranial skeleton. The holotype specimen includes one of the best-preserved squalodontid sterna known, and one of the most complete squalodontid vertebral columns known (29 vertebrae). Six additional specimens are referred to this species, including a skull and several mandible fragments from the Calvert Formation in Virginia and Maryland and the correlative Pungo River Formation in North Carolina. *Squalodon whitmorei* is larger than any other known squalodontid. It is not so common as *S. calvertensis*, which is found in the same deposits. *Squalodon whitmorei* appears to be most closely related to *Squalodon barbarus* (Mchedlidze, 1976) (originally described in *Kelloggia*, which is here considered a junior synonym of *Squalodon*).

INTRODUCTION

Tertiary marine strata exposed on the Atlantic Coastal Plain of North America have for many years produced fossils of large odontocetes, and a number of species were described from the 1850s to the 1920s. These include *Saurocetus gibbesii* Agassiz, 1848, and *Squalodon tiedemani* Allen, 1887; unfortunately, both were based on very fragmentary specimens, making it difficult to determine their taxonomic affinities.

Saurocetus gibbesii was based on a single tooth, possibly from Oligocene-age deposits in South Carolina. It is a posterior tooth, apparently originally with two roots, but differs in appearance from any described squalodontid tooth in that the enamel ornamentation is much simpler, with a small number of long, low ridges running from the base to the apex (Dooley, 2003).

Squalodon tiedemani was based on a partial rostrum collected during a dredging operation in the Wando River in South Carolina. The recognition of this species was of some importance, because *S. tiedemani* remains one of the largest non-physeterid odontocetes of (probable) Oligocene age, which makes it of particular paleoecological interest. In his review of the Squalodontidae, Kellogg (1923) was unable to decide whether *S. tiedemani* was a squalodontid or an archaeocete because of the holotype's large size and lack of posterior teeth.

Since Kellogg's (1923) review, most new material from large squalodontids has been referred (at least on specimen labels) to *S. tiedemani*, despite the indefinite status of the species. Even though specimens were being referred to the species, the small amount and poor preservation of the material prevented any decisions about the validity or relationships of *S. tiedemani*. Since 1923, *S. tiedemani* has been mentioned in the literature only a few times. Boreske *et al.* (1972) tentatively referred a Miocene specimen from North Carolina to this species. Later, Muizon (1994) used the name *S. tiedemani* for several specimens in an examination of squalodontid relationships; and Gottfried *et al.* (1994) cited Dooley (pers. comm.) in listing *S. tiedemani* among the fossil cetaceans from the Calvert Formation.

A potentially important specimen in the *S. tiedemani* puzzle is "Genus Y" of Whitmore & Sanders (1976, p.312). Sanders (1980) described this specimen as "the largest squalodont on record." The rostrum of "Genus Y" is quite similar in size and appearance, although not identical, to the holotype of *S. tiedemani*, and its posterior teeth are similar to the holotype tooth of *Saurocetus gibbesii*. "Genus Y" was found in an Oligocene unit near Charleston, South Carolina, the same area where both *Squalodon tiedemani* and *Saurocetus gibbesii* were found. Examination of "Genus Y" reveals a skull structure very different from that of *Squalodon*. Given their similarity of *Squalodon tiedemani* and *Saurocetus gibbesii* to "Genus Y", it is likely that neither is a squalodontid (Dooley, 2003).

Kellogg (1923) mentioned the existence of fossil remains of a large squalodontid from Maryland, but refrained from naming the material because it consisted of a single poorly preserved maxillary tooth. However, he did describe *Squalodon calvertensis*, a much smaller species based on a skull, dentary, and some postcranial material from the Calvert Formation of Maryland. Until now *Squalodon calvertensis* has remained the only North American squalodontid species based upon a skull.

In 1975, John D. Kunlo collected a partial fossil skeleton of a large squalodontid from the Miocene Calvert Formation in King George County, Virginia. The specimen was donated to the United States National Museum of Natural History, where Dr. Frank C. Whitmore, Jr., tentatively referred it to *S. tiedemani*, and it was given the number USNM 183023. The specimen has not been previously studied in detail. Given the probable Oligocene age of *Saurocetus gibbesii* and *Squalodon tiedemani*, and the probable non-squalodontid status of "Genus Y" from South Carolina, it is appropriate to designate the squalodontid from King George County as the holotype of a new species.

MATERIAL AND METHODS

A number of museums contain fairly extensive collections of vertebrate fossils from the North American Atlantic Coastal Plain. These collections were searched for fossil remains attributable to squalodontids. Because fragmentary fossils are often misidentified, all odontocete material was searched, rather than just squalodontid collections.

Institutions whose collections were examined, and their abbreviations:

AMNH—American Museum of Natural History, New York, New York

ANSP—Academy of Natural Sciences, Philadelphia, Pennsylvania

CMM-V—Calvert Marine Museum, Vertebrate Collections, Solomons, Maryland

MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

USNM—United States National Museum of Natural History, Smithsonian Institution, Washington, DC.

The fossils identified as pertaining to the new squalodontid species named herein were compared to fossils of other odontocetes in the collections of the above museums. Specimens used for comparison include: *Squalodon calvertensis* (USNM 10484 [holotype], USNM 10695, USNM 22902, USNM 23537, USNM 175382, USNM 328343, USNM 401547, CMM-V-208), *Eurhinodelphis bossi* (USNM 8842), and *Hadrodelphis calvertense* (CMM-V-11). In addition, published descriptions and photographs of the following taxa were used for comparison: *Kelloggia barbara* Mchedlidze, 1976, *Squalodon bariensis* (Jourdan, 1861) (Muizon, 1991), *Squalodon bellunensis* Dal Piaz, 1916 (Pilleri, 1985), *Phoberodon arctirostris* Cabrera, 1926, *Eosqualodon langewieschei* Rothausen, 1968a, and *Waipatia maerewhenua* Fordyce 1994.

Abbreviations: *ali*= basishpenoid; *aI* = incisor alveolus; *aC* = canine alveolus; *aP* = post-canine alveolus; *bo* = basioccipital; *boc* = basioccipital crest; C = upper canine; c = lower canine Ca = caudal vertebra; Ce = cervical vertebra; *eam* = external auditory meatus; *fpmx* = premaxillary foramen; *fr* = frontal; *fr/na* = frontal/nasal complex; *gf* = glenoid fossa; *hpp* = hamular process of pterygoid; I = upper incisor; i = lower incisor; L = lumbar vertebra; *max* = maxilla; *mlp* = medial lamina of pterygoid; *mpp* = medial part of palatine; *occ* = occipital condyle; *opc* = canal for optic nerve; P = upper post-canine; p = lower post-canine; *pal* = palatine; *pgp* = postglenoid process; *prp* = preorbital process of frontal; *pop* = postorbital process of frontal; *pmx* = premaxilla; *pt* = pterygoid; *scf* = subcircular fossa; *soc* = supraoccipital; *zps* = zygomatic process of squamosal; T = thoracic vertebra; *vo* = vomer.

SYSTEMATIC PALEONTOLOGY

Family SQUALODONTIDAE Brandt, 1873

Genus *Squalodon* Grateloup, 1840

Squalodon whitmorei sp. nov.

Diagnosis: A species of *Squalodon* with the following characteristics: cranium with condylobasal length greater than 1 m; alveolar row occupying at least 90% of rostrum length; glenoid fossa shallowly concave; postglenoid process relatively short vertically, wide transversely, and rounded; subcircular fossa very shallow; narrow tympano-squamosal recess; roots of anterior cheek teeth nearly circular in cross section; coronoid process of dentary large; diapophysis and parapophysis of atlas vertebra forming continuous ridge; axis vertebra with proximal half of parapophysis concave and distal half convex in anterior view; T2 centrum height less than 90% of centrum length; anterior spine present on diapophysis of T1; hypapophysis on Ce3 not bifurcate; widest part of all teeth proximal to base of crowns.

Holotype: USNM 183023: a cranium (lacking the basicranium, part of the left frontal, parts of both maxillae, most of the right side of the rostrum, and the occipital condyles, and with the squamosals detached); the proximal half of the left dentary; parts of ten teeth; portions of 29 vertebrae; the manubrium; and rib fragments, collected by John D. Kunlo, 1975.

Type Locality: King George County, Virginia, at the north end of Mason Mill Pond, the head of Machodoc Creek, 18 m above sea level, 2.6 km north of Edgehill (King George Quadrangle, 7.5' series) (Figure 1).

Formation and Age: The outcrop at Mason Mill Pond shows three distinct beds. The lowest stratigraphically is a dark green sandy clay, containing numerous casts of mollusks, especially bivalves. This is consistent with the lower Eocene Woodstock Member of the Nanjemoy Formation (Ward, 1992). Unconformably overlying the Nanjemoy Formation at this site is a lag deposit, approximately 0.3-0.5 m thick, containing reworked fossil gastropods and shark teeth, as well as quartz and phosphate pebbles. Immediately above the lag deposit is a white to pinkish clayey sand, at least 2m thick. The lithology and geographic position of the latter bed suggest that it represents the Fairhaven Member of the Calvert Formation ("Popes Creek Sand" of Gibson, 1983, see Ward, 1984, p. 57), which correlates with the Burdigalian and is late Early Miocene in age (Ward, 1992). Sediment still adhering to USNM 183023 indicates that it came from the latter layer. Other material from this locality included the following: six vertebrae, two periotics, a vertebral epiphysis, a supraorbital plate of the frontal, and various rib fragments from small odontocetes; two mysticete vertebrae; and teeth from the sharks *Odontaspis* sp. and *Isurus* sp.

Known range: Known only from the Fairhaven Member of the Calvert Formation in southern Maryland and northern Virginia, and from the age-correlative Pungo River Formation in North Carolina (Figure 1).

Referred specimens: Six, as follows: Paratype: USNM 424070, an isolated cranium, lacking the anterior part of the rostrum and most of the left squamosal, from King George County, Virginia, halfway between Machodoc Creek and Rosier Creek, 0.5 m above base of cliff on the Florance Property, Dahlgren, VA 7.5' quadrangle, 38° 17' 35" N 77° 2' W, collected by S. Thompson et al. in 1991, Fairhaven Member of the Calvert Formation; USNM 181575, partial rostrum and mandible with several broken teeth, from Beaufort County, North Carolina, at the Lee Creek Mine, collected by W. R. Walker in 1968, Pungo River Formation; USNM 23024, fragment of right dentary with a nearly complete cheek tooth, from King George County, Virginia, at Cleveland Grigsby's Bristol Farms, Rollins Fork, Rappahannock River, collected by James B. King on 10 August, 1939, unit unknown, but probably Fairhaven Member of the Calvert Formation; CMM-V-182, partial left dentary, from Charles County, Maryland, collected 27 April 1985, Fairhaven Member of the Calvert Formation, 3.75 m above the contact with the underlying Eocene Nanjemoy Formation; USNM 181643, right tympanic bulla, from King William County, Virginia, Mill Pond Creek (Gravitt's Mill Pond), collected in 1969 by Lauck W. Ward, Calvert Formation, Bed 12-14, but apparently reworked from an older unit; USNM 181644, right tympanic bulla, from Beaufort County, North Carolina, at the Lee Creek Mine, collected by J.W. Crawford, date unknown, Pungo River Formation.

Etymology : The species is named in honor of Dr. Frank C. Whitmore, Jr., employee of the U. S. Geological Survey at the USNM, who first identified the holotype as a squalodontid, and in recognition of his research on fossil cetaceans and his invaluable support of budding paleontologists.

DESCRIPTION AND COMPARISONS

Cranium: Cranial material includes the holotype USNM 183023 (Figure 2), paratype USNM 424070 (Figure 3), and USNM 181575 (Figures 5a-d). The reconstruction in Figure 4 is based on these specimens. Measurements of the crania are provided in Table 1.

The rostrum is relatively long (approximately 67% of the total condylobasal length), as in *S. calvertensis*. There is some warping of the rostrum in the holotype, but it appears that the narrowest point of the rostrum is immediately anterior to the mid-point of the rostrum, adjacent to the third maxillary alveolus. The premaxillae do not contact each other dorsally over the mesorostral groove. The lateral margins of the premaxillae are damaged distally, suggesting that they were somewhat expanded transversely. Muizon (1991, 1994) suggested that the latter character is a synapomorphy of the members of the Squalodontidae, although it appears to be absent in *Phoberodon arctirostris* (Cabrera, 1926).

As in *S. calvertensis*, the premaxillae are widest in dorsal view immediately posterior to the premaxillary foramina. In contrast to the holotype of *S. calvertensis* (UNSM 10484), they reach their maximum widths anterior to the mesethmoid, immediately anterior to the nares in the holotype of *S. whitmorei* (the mesethmoid is missing in the paratype). It should be noted, however, that the holotype of *S. calvertensis* is apparently a juvenile, so that its mesethmoid possibly was not ossified for much of its length. In both species, the premaxillae are much narrower posterior to the nasals and have posterior extensions that are fused to the frontal on the vertex.

The mesethmoid in USNM 183023 is ossified to a point 72 mm posterior to the premaxillary foramina. Foramina, apparently for the olfactory nerves, are present in the mesethmoid gutter and are continuous into the braincase.

There are no obvious sutures between the frontals and nasals, and no median sutures dividing the paired bones of each. The frontal-nasal complex is a large rugose mass of bone that bulges anteriorly on the midline, and has irregular, but mainly antero-posteriorly directed, grooves and ridges. The posterior ends of the premaxillae apparently also form part of this fused complex. The frontal-nasal complex is longer than wide, except along its posterior margin. The outline is rectangular for the anterior half, but posteriorly there is a strip of frontal that is exposed across the entire width of the nuchal crest. The frontals thus prevent the maxillae from contacting the supraoccipital in dorsal view. The parietal does not appear to be exposed on the dorsal surface of the cranial vertex.

The anterior margin of the frontal-nasal complex is convex in USNM 183023, suggesting that the nasals are still present as their anterior margins are convex in most primitive Odontoceti. Because no frontal/nasal sutures are visible, an estimate of the length of the nasals is impossible. The nasals appear to be missing in the paratype, USNM 424070. In a referred specimen of *S. calvertensis* (USNM 328343), the overall shape of the frontal-nasal complex is remarkably similar to that in *S. whitmorei*, and in the former specimen the nasals are definitely present, as the mesethmoid bone covers them anteriorly. In another specimen referred to *S. calvertensis* (USNM 10695), the frontal-nasal complex is damaged, and the frontal/nasal suture is present under the rugose surface.

As mentioned previously, the maxillae of *S. whitmorei* are separated from the supraoccipital in dorsal view by thin strips of the frontals. Mchedlidze (1984, p. 61) stated that the maxillae contact the supraoccipital in *S. calvertensis*, but this contradicts Kellogg's (1923) statement that they do not. My observations of the holotype (USNM 10484) of *S. calvertensis* support Kellogg's (1923) view, although the maxillae are almost in contact with the supraoccipital, being separated by approximately 2-3 mm of frontal. In an adult specimen referred to *S. calvertensis* (USNM 328343) the right maxilla appears to contact supraoccipital. Lack of a maxilla-supraoccipital contact may to a certain extent be a juvenile characteristic. This is supported by the structure of "Genus X" of Whitmore & Sanders (1976, Figs. 5 and 6), which is a primitive odontocete from Oligocene deposits of South Carolina, in which the maxillae contact the supraoccipital only in adult specimens.

As in other squalodontids, the maxillae of *S. whitmorei* are widest across the supraorbital processes of the frontals. Posterior to the supraorbital processes, the lateral margins of the maxillae are nearly straight in dorsal view, rather than being curved laterally as they are in more derived odontocetes. This results in the maxillae only partially covering the temporal fossae. There is a foramen on each side of the facial region in the middle of the ascending process of the maxilla, adjacent to the anterior margins of the frontal-nasal complex. Anterior of these foramina, the maxillae are poorly preserved in the holotype, USNM 183023, but in the paratype, USNM 424070, they are expanded laterally, almost completely covering the supraorbital plates of the frontals. The dorsal surface of the supraorbital plate of the frontal is completely preserved on the right side USNM 183023. The lateral edge of the frontal was not covered by the maxilla.

The antorbital notch is imperfectly preserved in both the holotype and paratype specimens, but it appears to be less deep and form a more obtuse angle than in the holotype of *S. calvertensis*. There are paired foramina on the maxillae, side by side, just posterior of the location of the premaxillary foramina, and another maxillary foramen located anterior to the level of the premaxillary foramina on each side. Anterior to these foramina, the maxillae are broad and smooth, and become gradually narrower transversely toward the tip of the rostrum. The anterior ends of the maxillae are not preserved, but they appear to end somewhere between the third and fourth alveoli counting back from the anterior end of the rostrum, as in *S. calvertensis* (USNM 23537).

The posterior part of the cranium of *S. whitmorei* is best preserved in the paratype, USNM 424070. The supraoccipital is similar in shape to that of the holotype of *S. calvertensis*. There is a prominent sagittal crest on the dorsal half of the supraoccipital in USNM 183023 that is not present on the paratype, USNM 424070. This crest is not present on the holotype of *S. calvertensis*, but is present in a specimen referred to *S. calvertensis* (USNM 328343). On *S. whitmorei* (USNM 183023) the upper third of the sagittal crest is very rugose, again in contrast to *S. calvertensis* (USNM 328343).

The lambdoidal crest is prominent in both species. The occipital condyles of *S. whitmorei*, apart from their larger size, are identical in shape to those of *S. calvertensis*, and the exoccipitals are also similar in shape to the holotype of *S. calvertensis*.

In lateral view, the rostrum of *S. whitmorei* is slightly curved dorsally. The curvature is less pronounced along the dorsal margin than it is ventrally. Kellogg (1923) noted the same feature in the holotype of *S. calvertensis* (USNM 10484). In *S. whitmorei*, the curvature is less pronounced than in *S. calvertensis*.

The most posterior alveolus of the holotype of *S. whitmorei* is about 51 mm anterior to the antorbital notch. This is relatively and absolutely much closer to the antorbital notch than in specimens of *S. calvertensis* (62 mm in USNM 10484, 65 mm in USNM 328343). In the paratype of *S. whitmorei* the position of the last alveolus is uncertain, but it is located less than 100 mm anterior to the antorbital notch.

The supraorbital process of the frontal is concave on both the dorsal and ventral surfaces, with a rounded preorbital process and a ventrally directed postorbital process. There is a large groove for the lachrimal in both the holotype and paratype, but the lachrimal itself is missing.

The temporal fossae are partially roofed over by the maxillae and the frontals. The anterodorsal portion consists of frontal, while the posterodorsal half consists of parietal. The suture between the frontal and parietal is mostly open in the holotype, but is fused in the paratype. The parietals are fused to the supraoccipital on their dorsal and posterior margins, contributing to the formation of the lambdoidal crest; ventrally they are fused to the squamosals.

The zygomatic processes are slightly ventrally directed. In lateral view they are convex on the dorsal margin and concave on the ventral margin. The left zygomatic process is longer than the right in the holotype, but both the left and right processes are detached from the skull and appear to be weathered. In the paratype the zygoma has a broad base and tapers rapidly to the tip. It also diverges laterally from the cranium in this specimen, whereas in *S. calvertensis* the zygoma is parallel to the sagittal plane of the cranium, or angled medially. However, in the paratype of *S. whitmorei* there appears to be some crushing of the skull, so this angle may not be accurate. For the same reason, the size of the gap between the postorbital process and the zygomatic process cannot be definitely determined.

The ventral side of the cranium is largely missing from the holotype of *S. whitmorei*, but it is partly preserved in the paratype. The tooth count is I3, C1, and P/M12, which is the same as in *S. calvertensis* (USNM 10484, USNM 23537). The alveoli for the incisors indicate that the roots of the incisors were approximately circular in cross section and oriented procumbently, in the typical squalodontid fashion (Muizon, 1991). The alveolus for I1 indicates that this tooth was directed nearly straight anteriorly, and at least part of its alveolus is directly dorsal to the alveolus for I2. Only the anterior portion of the left alveolus for the canine is preserved in USNM 183023, but its root appears to be nearly circular in cross section as well.

Table 1.– *Squalodon whitmorei*, sp. nov., measurements of crania (in mm).

	USNM 183023	USNM 424070
Total length of cranium as preserved	1159+	1069+
Length of rostrum as preserved	782	596+
Width across supraorbital processes	337	330
Total height of cranium	--	200
Height at rostrum base	115	115
Length of maxilla (left/right)	898+/846+	940+/856+
Width across premaxillae at anterior end of mesethmoid	127	--
Width across premaxillae at anterior end of nasals	110	142
Maximum width premaxilla anterior to mesethmiod (left/right)	52/51	58/53
Minimum width premaxilla (left/right)	20/--	22/22
Width of rostrum across antorbital notches	149+	268
Width of rostrum at narrowest point	108	123
Length of supraorbital process (left/right)	-/274	261/262
Maximum width of supraorbital process (left/right)	61+/64+	70+/90+
Minimum width of premaxillae on vertex	92	120
Maximum thickness of preorbital process (left/right)	--/38	34/33
Maximum diameter of occipital condyle (left/right)	--/--	72/--
Width across basioccipital crests	--	155+
Maximum width of supraoccipital	234	203
Total length of vomer	432+	600
Length of frontal on vertex (left/right)	--/--	88/93
Width across exposed posterior frontal	202	135+
Length of frontal/nasals medially	94	--
Distance from last alveolus to antorbital notch	51	100

The anterior maxillary alveoli in the holotype of *S. whitmorei* indicate that the first three post-canine tooth roots were circular in cross section, while the fourth tooth root was slightly compressed transversely, and the fifth circular. There is a slight trace of a vertical ridge within the alveolus of the fifth post-canine tooth in the holotype, and this possibly divided the remnants of two roots. This alveolus is not sufficiently preserved in other North American *Squalodon* specimens to determine its presence or absence.

The seven posterior maxillary teeth all possessed two roots, based on the shapes of the alveolae. However, it is not clear if any of the roots of these teeth were separated for their entire length. The three posterior-most alveoli have septa for their entire length, but they are all broken transversely in the holotype, and this area is not well preserved in the paratype. Each of these seven alveoli is transversely compressed.

While most of the maxillary alveoli are transversely compressed, they are all much less transversely compressed than are the corresponding alveoli in any specimen of *S. calvertensis*. In both species the teeth anterior of the fifth post-canine tooth appear to have been directed increasingly laterally. There are no well-preserved incisor alveoli from *S. calvertensis*, but isolated squalodontid incisors in the USNM collection possibly belong to this species and are nearly circular in cross-section.

In ventral view, the premaxillae are visible along the medial sides of the maxillae from the anterior end of the rostrum to the level of the ninth maxillary tooth. Anteriorly the premaxillae comprise the entire tip of the rostrum anterior to the canines, and they remain in midline contact with each other posteriorly to a point adjacent to the third or fourth maxillary tooth. From this point the vomer is exposed along the palate posteriorly to the eleventh maxillary tooth. Posterior to the eleventh tooth the maxillae come into contact on the midline.

On the midline of *S. whitmorei*, the maxillae extend back to approximately the level of the antorbital notch (as revealed by the damaged right palatine in the holotype). The maxillae have the appearance of a triangle, whose apex is pointed posteriorly, where they come into contact with the palatines.

The pterygoids are missing from the holotype. In the paratype the pterygoids are present, but the sutures between the pterygoids and palatines, and between the palatines and the maxillae, are partly obscured. In contrast to Muizon's (1994) statement about *Squalodon tiedemani* (= *S. whitmorei*), rugose areas on the palatines in the holotype indicate that the pterygoids did not contact the maxillae, and only partially covered the palatines. This is in contrast to the condition in *Squalodon bariensis*, in which the pterygoids contact the maxillae, dividing the palatines into two parts (Muizon, 1994). Muizon (1991, 1994) considered the condition in *S. bariensis* to be ancestral to the condition in *Platanista*, in which the pterygoids completely cover the palatines on the midline. However, the presence of the *S. bariensis* condition in at least some specimens of *Globicephala*, and the variation in the anterior extent of the pterygoids in other delphinids, suggest that this character is too variable to be useful in systematics.

The hamular processes of the pterygoids of the paratype are large and curve sharply medially. Posterior to the nares, the medial laminae of the pterygoids extend posterolaterally until they contact the basioccipital crests. This is similar to the condition in *S. calvertensis* (USNM 328343) and *S. bariensis* (Muizon, 1991). The lateral lamina of the pterygoid is broken, but appears to have come into contact with the falciform process of the squamosal, so that the pterygoid sinus was surrounded on both sides by the pterygoid. This is again consistent with the condition in *S. calvertensis* and in *S. bariensis* (Muizon, 1991).

Posterior to the frontals, the roof of the braincase is exposed in the holotype, revealing the parietals, which are poorly sutured to the frontals and fused to the supraoccipital. Paired depressions, apparently for the olfactory lobes, are present at the anterior mid-line margin of the braincase. These depressions are large (about 40 mm in length) and have foramina open into the mesorostral gutter. There is a distinct septum dividing the two depressions, and the right depression is larger than the left.

Some details of the ventral side of the squamosal are preserved in detached squamosal fragments of the holotype (Figure 6). In ventral view, the glenoid fossae are shallow depressions. The postglenoid process is rounded and relatively short ventrally. In contrast to *S. calvertensis*, the postglenoid process runs along almost the entire length of the anterior meatal crest. Medial to the glenoid fossa is a crest, running from the alisphenoid-squamosal suture to the anterior meatal crest. This creates a narrow shelf between the glenoid fossa and the subcircular fossa, 5 mm wide at its posterior end, which apparently corresponds to the tympano-squamosal recess. There is a foramen in the anterior part of this recess. The recess is much narrower than in *S. calvertensis* (USNM 23537).

The articulation for the tympanic bulla is relatively simple, with two troughs separated by a low ridge. There is no indication of spongy bone in this area, or of fusion with the posterior process of the tympanic bulla.

A large, shallow subcircular fossa, more shallow than the subcircular fossa in *S. calvertensis* (USNM 23537), is located dorsomedially to the spiny process. There is a single large foramen in the posterior part of the fossa. At the anterior end of the fossa is a groove leading to the foramen spinosum. This groove continues to the foramen ovale. In the holotype, a large protuberance is located immediately posterior of the foramen spinosum, within the subcircular fossa; it is unclear whether or not this protuberance is present in the paratype. It is not present in *S. calvertensis*. The medial margin of the subcircular fossa consists of a massive bone, which may represent the parietal. The anterior part of this bone is a ridge leading medially from the subcircular fossa, while the posterior part is a groove oriented parallel to the ridge.

Tympanic bulla: Tympanic bullae and periotics were not preserved from any of the known crania of *S. whitmorei*. There are, however, two isolated tympanic bullae that may represent this species (Figures 5e-h). The two specimens are both heavily abraided and damaged, but the preserved portions resemble the tympanic bulla of *S. calvertensis* (USNM 328343) in most respects, except that they are approximately 50% larger. The specimens are also the appropriate size for *S. whitmorei*, assuming that the size proportions of cranium to bulla are the same for both species.

The tympanic bulla is heart-shaped, with two lobes posteriorly. As noted by Muizon (1991) in redescribing *S. bariensis*, the two lobes are the same length with a narrower lateral lobe. The lobes are separated by a ventral groove that extends about half the length of the bulla and ends in a roughened area. It is unclear whether or not an anterior bullar spine was present in *S. whitmorei*, due to the heavy abrasion of both of the available specimens. The outline of the lateral margin of the bulla is a smoothly convex curve from the anterior to posterior end; there is no prominent antero-lateral notch or convexity (*sensu* Muizon 1987, 1991), as is present in both *S. calvertensis* and *S. bariensis*.

The involucrum is present only in the posterior half of the bulla, in contrast to the relatively much larger involucrum in *S. calvertensis* and *S. bariensis*. There are a number of coarse striations on the dorsal margin of the involucrum that extend onto the inner face, which are also present in *S. calvertensis*, *S. bariensis*, and *Waipatia maerewhenua*. Fordyce (1994) interpreted these striations as being associated with the peribullary sinus tissues.

Mandible: The posterior portion of left dentary of the holotype of S. *whitmorei* (Figure 7) is preserved, including the last eight alveolae; the coronoid process and large portions of the pan bone are missing. Referred dentaries of S. *whitmorei* include CMM-V-182 (Figure 8a-c), USNM 23024 (Figure 8d-f), and USNM 181575 (Figure 5b-d); measurements are provided in Table 2.

Compared to the left dentary of S. *calvertensis* (USNM 22902), the alveoli of S. *whitmorei* are less flattened transversely, as is the case with the maxillary teeth. The condyle is relatively larger in S. *whitmorei* (USNM 183023), and the outer margin of the condyle is convex (it is concave in S. *calvertensis* [USNM 22902]). It appears that the mandible was relatively narrower across the condyles than in S. *calvertensis*, but this could be due to crushing. There are four small nutrient foramina on the lateral surface. Three are in a line ventral to the most posterior alveolae with the fourth is posterior to the last alveolus. There is a large tuberosity internally at the level of sixth alveolus (counting forward), roughly corresponding to the posterior end of the symphysis, which is also present in S. *calvertensis* (USNM 22902). This seems to be the thickest part of the dentary, and most of the isolated specimens of S. *whitmorei* dentaries include this tuberosity.

In the holotype of S. *whitmorei* the sixth tooth (counting forward) has roots that are fused for nearly their entire length. However, in referred specimens USNM 23024 and CMM-V-182, this tooth had roots that were separated for nearly their entire length (based on either the tooth itself or the septum in the alveolus). Because these three specimens are in all other respects similar to USNM 183023, it appears that there is some variation in tooth structure within S. *whitmorei*.

Table 2.–*Squalodon whitmorei*, sp. nov., measurements of dentaries (in mm). L = left, R = right, Sym. = mandibular symphysis.

Catalog Number	Side	Total length	Maximum height	Minimum thickness of tooth row	Minimum width of tooth row	Maximum width of tooth row	Height at last tooth
USNM 23024	R	527+	--	–	45-	68+	--
USNM 181575	L&R	389+	--	--	--	--	--
USNM 183023	L	848+	295+	85	53	60	93
USNM 243909	Sym.	125+	--	--	–	46++	--
CMM-V-182	L	543+	78+	--	51-	–	--

Teeth: The teeth of S. *whitmorei* possess very large roots, with the widest part of the tooth well below the base of the crown. In contrast, in S. *calvertensis* the widest part of each tooth is usually at or very near the base of the crown. The crowns of the post-canine teeth in these two species are essentially the same size and have the same enamel texture.

Portions of 11 S. *whitmorei* teeth are known (Figure 9, Table 3); ten of these are associated with the holotype. These include the roots of the three upper left incisors, the root of the upper left canine with a fragment of the crown, the roots and partial crown of the seventh upper left post-canine tooth, the roots and most of the crown of the sixth lower left tooth (counting forward), and partial roots of three other lower left teeth. A single tooth is also included as part of the referred specimen, USNM 23024.

The root of the left I1 (Figure 9a) can be removed from its alveolus. It is straight, and nearly circular in cross section. The base of the root of I2 is imbedded in the alveolus; it is slightly flattened dorsoventrally. The base of the root of I3 is also imbedded in the alveolus and is circular in section. The root of the canine (Figure 9b-c) is nearly as long as that of the I1, but it is somewhat curved. A small portion of the crown is preserved. It is covered with a thin layer of enamel that is longitudinally striate (*cristae rugosa* of Rothhausen, 1968). The striations are much finer and more numerous than on the teeth of the holotype of S. *calvertensis* (USNM 10484), although other specimens of S. *calvertensis* (for example, USNM 328343) show a wide range of enamel ornamentation, sometimes approaching that seen in S. *whitmorei* (USNM 183023). The seventh upper left post-canine tooth is imbedded in the alveolus. A partial crown is present, but it is too poorly preserved to determine any details.

Because the anterior part of the dentary is not known for S. *whitmorei* the lower tooth positions are designated by counting forward from the posterior end. The sixth lower left tooth (Figure 9d-f) is the best-preserved tooth (this is in the position of the thickest part of the dentary). The roots are bent posteriorly at their tips and are joined for nearly their entire length. They are indistinguishable from each other about 7 mm below the base of the crown. The crown is covered with enamel of the same texture as the canine. The cristae rugosae become finer toward the apex of the crown. There was possibly one posterior denticle, now

Table 3.--*Squalodon whitmorei*, sp. nov., tooth measurements in mm. See p. 6 for abbreviations.

Catalog Number	Position	Crown Length	Crown Width	Crown Height	Overall Height	Roots
USNM 10694	Left P	25	15+	29+	66+	2 fused top 1/3
USNM 23024 (1)	Right p4 ?	18+	14	23+	70+	2 fused
USNM 23024 (2)	Right p7 ?	26	14	28+	72+	2 fused top 1/2
USNM 183023 (1)	Left I 1	--	--	--	102+	1
USNM 183023 (2)	Left C	18+	17	9+	96+	1
USNM 183023 (3)	Left p7	28	16	22+	85+	2 fused

broken, and there is a longitudinal ridge on both cutting edges, lined with heavily worn serrations.

The posterior root of the fifth lower left tooth is short and thick (Figure 9g-h). It was apparently separate from the anterior root for most of its length, but the two roots appear to have been joined below the crown. The thickest part of the root is 9 mm below the top as preserved. The tooth in this same position in the dentary is also preserved in USNM 23024 (Figure 9k-m), and its crown is essentially the same in both shape and enamel texture as the sixth lower left tooth in USNM 183023, however, the roots are separated, in contrast to USNM 183023. The posterior root of this tooth is similar in shape to that of the fifth lower tooth in USNM 183023.

Only the base of the anterior root of the fourth lower left tooth is preserved (Figure 9i-j). It is rectangular in cross section, and the tip of the root is recurved. The thickest part of the root is 18 mm below the top of the preserved portion. The anterior root of the third lower left tooth is also rectangular in cross section.

Sternum: The manubrium of USNM 183023 (Figure 10) is a large "T"-shaped bone, 200 mm in length and 192 mm in maximum width. Its dorsal surface is concave and its ventral surface is convex, except at the cross of the "T" where it is concave ventrally. There appear to be articulations for three ribs on each side, all on the cross of the "T." The posterior margin suggests that there was at least one sternebrum posterior to it.

The only other known squalodontid sternum from North America is a fragment with a referred specimen of *S. calvertensis* (USNM 175382). Despite its poor preservation, this specimen is remarkably different from that of *S. whitmorei*. Although the fragment suggests a bone comparable in relative size to the same element in *S. whitmorei*, it is only about one-half as thick. There are likewise three rib articulations on each side, but in *S. calvertensis* these articulations seem to be distributed along the entire side of the sternum, rather than crowded together at the anterior end.

Ribs: There are 21 separate rib fragments preserved with USNM 183023, of which six are identifiable as left ribs and five as right ribs (Figure 11). One of the fragments, apparently the first right rib, has the tuberculum preserved. The tuberculum is 25 mm long and deeply concave. This rib abruptly curves medially at about 150 mm distally from the tuberculum. A similar curvature is also present in several other rib fragments. All of the rib fragments are consistent in shape with various *S. calvertensis* ribs in the USNM and CMM-V collections, and with odontocete ribs in general

Cervical vertebrae: Measurements of the cervical vertebrae are listed in Table 4. The atlas vertebra (Figure 12) is similar to that of *S. calvertensis* (USNM 175382). The diapophyses and parapophyses form a continuous ridge on USNM 183023 whereas they are separate in *S. calvertensis*. The neural spine is relatively longer in *S. whitmorei* than it is in *S. calvertensis*.

The axis vertebra of *S. whitmorei* (Figure 13) is also similar to that of *S. calvertensis* (USNM 328343), from which it differs by having postzygopophyses that are relatively much larger compared to the centrum, and a less tapered odontoid process. The ridge on the top of the transverse process is smoothly concave in *S. calvertensis* whereas in *S. whitmorei* the proximal half is concave and the distal half convex. The diapophyses are relatively much larger in *S. whitmorei* than they are in *S. calvertensis*. The apex of the neural spine is expanded transversely, rugose and asymmetrical in *S. whitmorei*.

The third cervical vertebra of *S. whitmorei* (Figure 14a-e) is complete except for the neural arch and spine and most of the transverse processes. Both epiphyses are fused to the centrum. The diapophyses and parapophyses on each side form a continuous ridge at their bases, as in *S. calvertensis* (USNM 23537 and 328343); vertebrarterial canals are not present. This is apparently a diagnostic character for identifying Ce3 in both *S. whitmorei* and *S. calvertensis*. However, there is a small (6 mm diameter) canal on the left side of Ce3 of *S. whitmorei* that is not present on either specimen of S.

calvertensis. The hypapophysis of *S. whitmorei* is not bifurcated, as it is in both specimens of *S. calvertensis*.

The fourth cervical vertebra of *S. whitmorei* (Figure 14f-j) is complete except for the neural arch and spine and most of the transverse processes. The anterior epiphysis is fused to the centrum, but the posterior epiphysis was not fused. Because epiphysis fusion had only progressed to the fourth cervical vertebra, the specimen was not mature. There are distinct vertebrarterial canals present on each side with a dorsoventral diameter of 15 mm. In both *S. calvertensis* and *S. whitmorei*, Ce4 is the first cervical vertebra to have distinct vertebrarterial canals.

Two parapophyses appear to be from Ce5 and Ce6 (Figure 14k-l), based on a comparison with *S. calvertensis* (CMM-V-208). There are no significant differences between *S. calvertensis* and *S. whitmorei* in these vertebrae. No seventh cervical vertebra is known for *S. whitmorei*.

Table 4.--*Squalodon whitmorei*, sp. nov., holotype USNM 183023, vertebra measurements (in mm). See p. 6 for abbreviations. * = epiphyses missing, not included in measurement. + = bone was damaged, measurement is as preserved.

Position	Maximum height	Neural canal maximum width-posteriorly	Neural canal maximum height-anteriorly	Neural canal maximum height-posteriorly	Centrum height-posteriorly	Centrum width-posteriorly	Centrum length with (*without) epiphyses	Width between tips of parapophyses	Width between tips of prezygopophysis	Height of neural spine	Width between tips of diapophyses	Length-left postzygopophysis to left prezygopophysis	Length-right postzygopophysis to right prezygopophysis	Length-neuropophyses	Length-neural spine at base
Atlas	149	72	80	74	72	--	--	152	--	39	163	--	--	--	55
Axis	179	64	52	40	40	119	45	212	--	58	140	--	--	--	80
Ce3	88+	--	--	--	--	92	34	127+	--	--	111+	--	--	--	--
Ce4	87+	--	--	--	--	92	40	116+	--	--	109+	--	--	--	--
T1	--	51+	--	--	--	--	--	--	--	41+	82+	--	--	--	61
T2	102+	56	35+	31+	29+	110	62*	--	115	--	183+	--	--	--	--
T3	--	54	39+	38+	38+	--	--	--	--	74+	139+	93	--	32+	80
T4	112+	52+	40+	37+	37+	99	72	--	--	--	124+	--	--	--	--
T5	151+	46+	22+	24+	24+	102	74*	--	--	62+	83+	--	--	34+	75
T6	179+	45	52	50	50	100+	79	--	76+	62+	115+	114	89+	50+	95
T7	--	40+	24+	25+	--	--	--	--	46+	32+	96+	--	118	--	97
T8	89+	--	--	--	--	89+	78*	--	--	--	125+	--	--	--	--
T9	92+	44	--	--	--	98	94	155+	--	--	--	--	--	--	--
T10	99+	43	25+	20+	19+	99	101	141+	--	--	--	--	--	--	--
T11	98+	42	19+	18+	18+	101	104	192+	--	--	--	--	--	--	--
L1	101+	41	20+	16+	16+	102	109	142+	--	--	--	--	--	--	--
L2	102+	38	18+	19+	21+	103	109	311+	--	--	--	--	--	--	--
L3	308+	35	59	44	44	106	113	268+	--	158+	--	--	--	24	94
L4	112+	33	10+	11+	11+	109	116	349+	--	--	--	--	--	--	--
L5	314+	32	56	43	43	109	115	359+	--	161+	--	--	--	--	93
L6	309+	26	45	43	43	110	112	339+	--	164+	--	--	--	--	71+
Ca"1"	113+	23	--	19+	19+	109	114	264+	--	--	--	--	--	--	--
Ca"2"	138+	20	22+	17+	17+	112	108	249+	--	--	--	--	--	--	--
Ca"3"	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Ca"4"	155	19	12	11	11	105	104	154	--	13	--	--	--	--	35
Ca"5"	133	18	14	11	11	95	99	114	--	14	--	--	--	--	38
Ca"6"	101	6	5	5	5	82	84	102	--	--	--	--	--	--	--

Thoracic vertebrae: Portions of 11 thoracic vertebrae are preserved (Figures 15-21). The thoracic vertebrae of *S. whitmorei* are generally very similar to the corresponding vertebrae of *S. calvertensis* (USNM 23537). There is a distinct anterior spine on the diapophysis of T1 and T2. In *S. calvertensis* (USNM 23537) this spine is present only on T2. In *S. whitmorei*, the centrum of T2 is 33% longer relative to its height than it is in *S. calvertensis* (USNM 23537). Rib articulations are located on the diapophyses of T1-T7. The diapophyses in T1-T7 angle anteriorly in dorsal view. As in *S. calvertensis*, in posterior view the diapophyses on T1 are sharply angled ventrally, while on T2 to T4 they are horizontal and on T5 to T7 they are angled dorsally. From T8-T11 the rib articulations are on parapophyses; the parapophyses all angle posteriorly. There are articulations for the tubercula high on the centra of the first six thoracic vertebrae (the centra of T1 and T3 are not preserved). The articulations are about equally prominent on both the anterior and posterior margins of the centra. The centrum of T7 is not preserved, but T8-T11 do not possess articulations for tubercula. The centra of T2, T4, and T5 each have at least one free epiphysis; the centra of T1 and T3 are not preserved. The centra are "heart-shaped" in anterior view, becoming progressively more circular in the more posterior vertebrae. This trend is essentially complete by T11; the centrum of this vertebra is very similar to that of the first lumbar, but is considered a thoracic because is lacks the sharp-edged hypapophysis found in the lumbar vertebrae (the ends of the transverse processes are missing).

Lumbar vertebrae: Six lumbar vertebrae preserved with USNM 183023, apparently L1-L6 (Figures 21-26). Unfortunately, there is no complete lumbar series from *S. calvertensis* available for comparison. In addition, there are six isolated neural spines that may be from either lumbar vertebrae or from thoracic vertebrae (Figure 27).

The six lumbar vertebrae are all very similar to each other, and to isolated lumbar vertebrae from *S. calvertensis* (USNM 22902 and 10484), as well as to T11. All have tall neural spines when preserved, and large parapophyses and metapophyses. They have much sharper and more prominent hypapophyses than do the posterior thoracic vertebrae. The parapophyses project straight laterally from the centra, in both dorsal and anterior views. In dorsal view the parapophyses are rectangular in outline, with almost no taper at their tips. Unlike the caudal vertebrae, the hypapophyses are not split to articulate with chevrons.

Caudal vertebrae: The preserved caudal vertebra series of the holotype of *S. whitmorei* includes six non-consecutive vertebrae (Figures 28-30), and is too incomplete to determine the absolute position of each vertebra in the series. Because no vertebra was adjacent to any of the others, there were at least 11 caudal vertebrae.

One of these vertebrae may be Ca1 (Figure 28a-e), based on the size of its centrum and neural canal compared to the sixth lumbar vertebra. In general appearance this vertebra is very similar to L6. The parapophyses, while still rectangular in outline and oriented as in the lumbar vertebrae, are shorter.

The next four preserved caudal vertebrae all have numerous foramina running through the centra and the bases of the processes, and each has large articulations for the chevrons (except for the third in the series, in which the centrum is not preserved). The second vertebra in this series (Figure 28f-j) has parapophyses that are angled anteriorly and ventrally, and taper toward the tips. In the three most posterior caudal vertebrae, the parapophyses are reduced to small ridges. The sixth vertebra (Figure 30f-j) is typical of near-terminal caudal vertebrae of Cetacea.

Two elements may be interpreted as chevrons; one of these (Figure 30k-n) is subrectangular in lateral view, and broadens somewhat ventrally. In anterior view, it tapers ventrally. The other specimen (Figure 30o-s) is "saddle-shaped", with a broad ventral surface that is convex at each end and concave in the middle. In both specimens the dorsal part of the bone is missing.

RELATIONSHIPS

A problem in squalodontid taxonomy is the possibility of synonymy because of the large number of species that have been based on poor material, and the possibility of age, sexual, or individual variability. This problem is compounded by the similarities among the known squalodontid specimens. A complete review of squalodontid systematics is beyond the scope of this paper, but it is informative to examine the degree of similarity of *Squalodon whitmorei* to other described species.

The largest previously described squalodontid was *Kelloggia barbarus* Mchedlidze, 1976, from Late Oligocene strata of Azerbaidzhan (Mchedlidze, 1984). Mchedlidze named the genus *Kelloggia* primarily on the basis of two features.

First, the supraorbital processes of the maxillae of *Kelloggia* were described as more completely covering the temporal fossae than in any other known squalodontid. However, the edges of the supraorbital processes of the maxillae are very prone to damage, and in most specimens they are at least partially missing. A specimen of *S. calvertensis* (USNM 328343) has more extensive supraorbital processes of the maxillae than does *Kelloggia barbarus*.

A second character in defining the genus *Kelloggia* was the shape of the rostrum, described by Mchedlidze as differing from *Squalodon* spp. as being broad for its entire length, with the implication that it lacked a constriction (or that the distal end of the rostrum was not laterally inflated). The rostrum of *Kelloggia barbarus* is badly crushed, but is clearly constricted at about mid-length, as figured by Mchedlidze (1984, Plates XXX and XXXI). Relative to the size of the cranium, the rostrum of *Kelloggia* is of comparable breadth to those of *S. bariensis* and *S. calvertensis*, and narrower than it is in *S. whitmorei*.

As neither of these characters serves to reliably distinguish the two genera, I consider *Kelloggia* to be a junior subjective synonym of *Squalodon*, new synonomy.

Squalodon barbarus (Mchedlidze, 1976), new combination, is more similar to *S. whitmorei* than it is to any other squalodontid. Both are relatively large, although the skull of *S. barbarus* is only about 80% the length of the skull of *S. whitmorei*. *S. barbarus* has similarly expanded tooth roots as *S. whitmorei*. In *S. barbarus*, the glenoid fossa is more deeply concave, and the postglenoid process is more pointed, than in *S. whitmorei*. In *S. barbarus*, the alveolar row does not extend as far proximally on the rostrum, the atlas does not have a lamina connecting the parapophyses to the diapophyses, and the axis does not have the unusual parapophysis shape present in *S. whitmorei*. *Squalodon barbarus* has 14 upper post-canine teeth, compared to only 12 in *S. whitmorei*.

Other squalodontids, while bearing a strong resemblance to *S. whitmorei*, are not as similar as is *S. barbarus*. *Squalodon whitmorei* differs from *S. calvertensis* in the following characters: 1) larger size; 2) alveolar row ends closer to the antorbital notch; 3) postglenoid process rounded and not as long; 4) roots of anterior maxillary teeth almost circular in cross section; 5) coronoid process of mandible relatively much larger; 6) diapophysis and parapophysis of atlas forming a continuous ridge; 7) on axis, proximal half of parapophysis concave and distal half convex; 8) second thoracic vertebra centrum longer relative to its height; 9) anterior spine on diapophysis of T1 present; 10) hypapophysis on Ce3 not bifurcate, 11) roots very large relative to crown, with the widest part of the tooth always well below the base of the crown instead of at the base of the crown, 12) subcircular fossa more shallow, 13) tympano-squamosal recess very narrow.

Squalodon bariensis is very similar to *S. calvertensis*. *Squalodon whitmorei* differs from *S. bariensis* in characters 1, 3, 4, and 11 as listed above for *S. calvertensis*.

Phoberodon arctirostris Cabrera, 1926 and *Eosqualodon langewieschei* Rothausen, 1968a are both large species whose crania are nearly 1 m in length, but are still smaller than *S. whitmorei*. *Phoberodon arctirostris* differs from *S. whitmorei* in characters 6, 8, 9, and 11 listed above. In *Eosqualodon langewieschei* the external nares are essentially level with the orbits (Rothausen, 1968a), a diagnostic character of the genus *Eosqualodon*. In *S. whitmorei* and other species of *Squalodon*, the external nares are located posterior to the level of the orbits. Moreover, the exposure of the parietals in dorsal view in *Eosqualodon* (Rothausen, 1968b) is absent in *S. whitmorei*, although Whitmore & Sanders (1976) indicated that this character may be subject to considerable ontogenetic variation.

The presence of an upturned rostrum was first described by Kellogg (1923) in the holotype of *S. calvertensis*, and is most pronounced in that specimen. Kellogg was uncertain whether the curvature was present in the living animal or was due to postmortem warping.

This character is broadly but not universally distributed among squalodontid specimens, although the degree of upturning is generally slight. It is slightly expressed in the holotype of *S. whitmorei*, although there is some crushing and deformation of the rostrum of this specimen. The cranium of *S. barbarus* is too badly crushed to determine the presence or absence of this character. It appears to be present in at least some specimens of *S. bariensis* (Muizon 1991, Fig. 8), *Eosqualodon langewieschei* (Rothausen, 1968a, Plate 11.1), and *Phoberodon arctirostris* (Cabrera, 1926, Fig. 9). Moreover, Wyman (1850) described a dentary fragment from Richmond, Virginia, which may be from a squalodontid and which is dorsally curved at the tip. This condition is also present in some dentaries referred to *S. calvertensis*, for example USNM 22902 and USNM 401547. However, many of the specimens figured by Pilleri (1985, Plates I, II, VII, X, XI, XII) from the Belluno Sandstones do not appear to have upturned rostra. Given the uncertain distribution and expression of this character, it is of questionable usefulness in systematic studies.

As with the upturned rostrum, there are uncertainties in the distribution and significance of the distally inflated rostrum. This feature was apparently present in the holotype of *S. whitmorei*, based on the damaged anterolateral margins of the premaxillae. It is present in *Squalodon bellunensis* Dal Piaz, 1901 (Pilleri, 1985, Plate VI), and *S. barbarus* (Mchedlidze, 1984, XXX and XXXI). It is present in some specimens referred to *S. bariensis* (Muizon, 1991, Fig. 9), but not others (Pilleri, 1985, Plate I). The distal end of the rostrum is not well preserved in any specimens of *S. calvertensis*. A distally expanded rostrum was apparently not present in *Phoberodon arctirostris* (Cabrera, 1926, Fig. 10), nor in *Eosqualodon langewieschei* (Rothausen, 1968, Fig. 2b).

Muizon (1991, 1994) suggested that a distally expanded rostrum is a synapomorphy of the Squalodontidae, but its absence in *Phoberodon* and *Eosqualodon* rule this out. There is a possibility that the distally expanded rostrum is a synapomorphy of the genus *Squalodon*, but its absence in some specimens of *S. bariensis* leaves this open to doubt. It appears that the distal end of the rostrum is expanded to accommodate the enlarged first incisors, suggesting the possibility that this character is subject to sexual dimorphism or ontogenetic variation.

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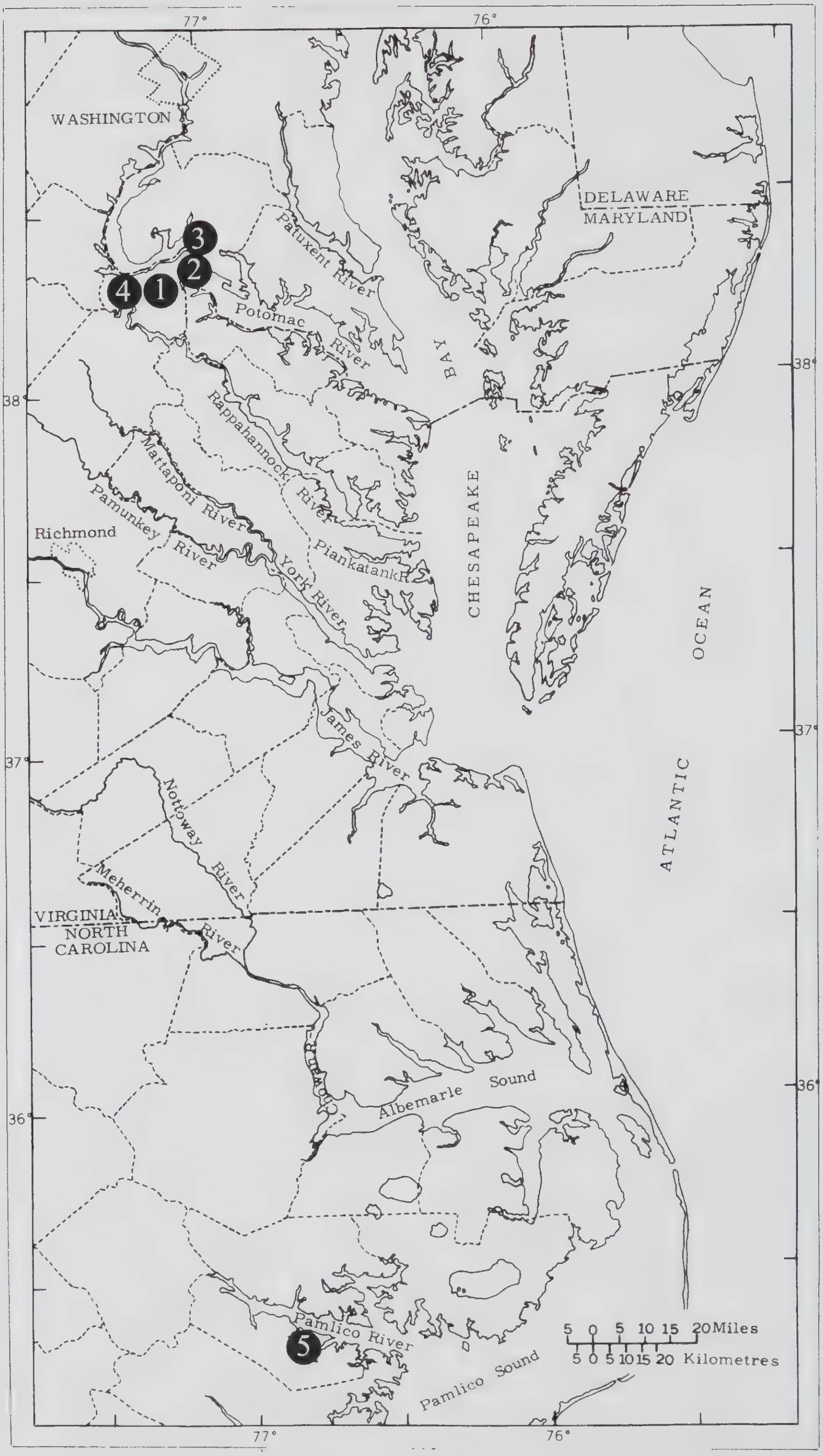

Figure 1.–Map of Chesapeake Bay area showing localities for specimens of *Squalodon whitmorei*, sp. nov. 1, USNM 183023, holotype. 2, USNM 424070, paratype. 3, CMM-V-182. 4, USNM 23024. 5, USNM 181575.

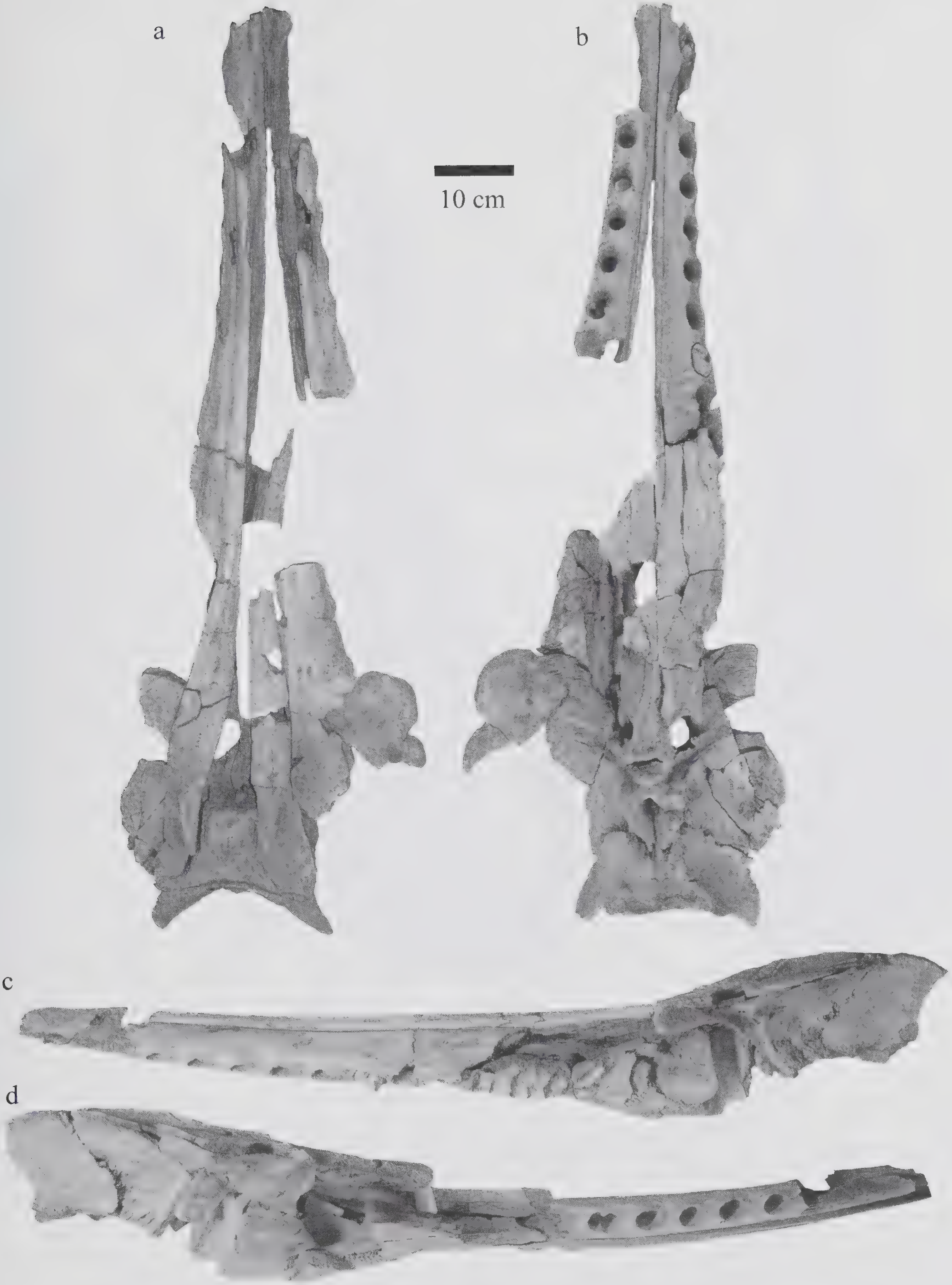

Figure 2.–*Squalodon whitmorei*, sp. nov., holotype cranium, USNM 183023. a, dorsal view; b, ventral view; c, left lateral view; d, right lateral view. Scale = 10 cm.

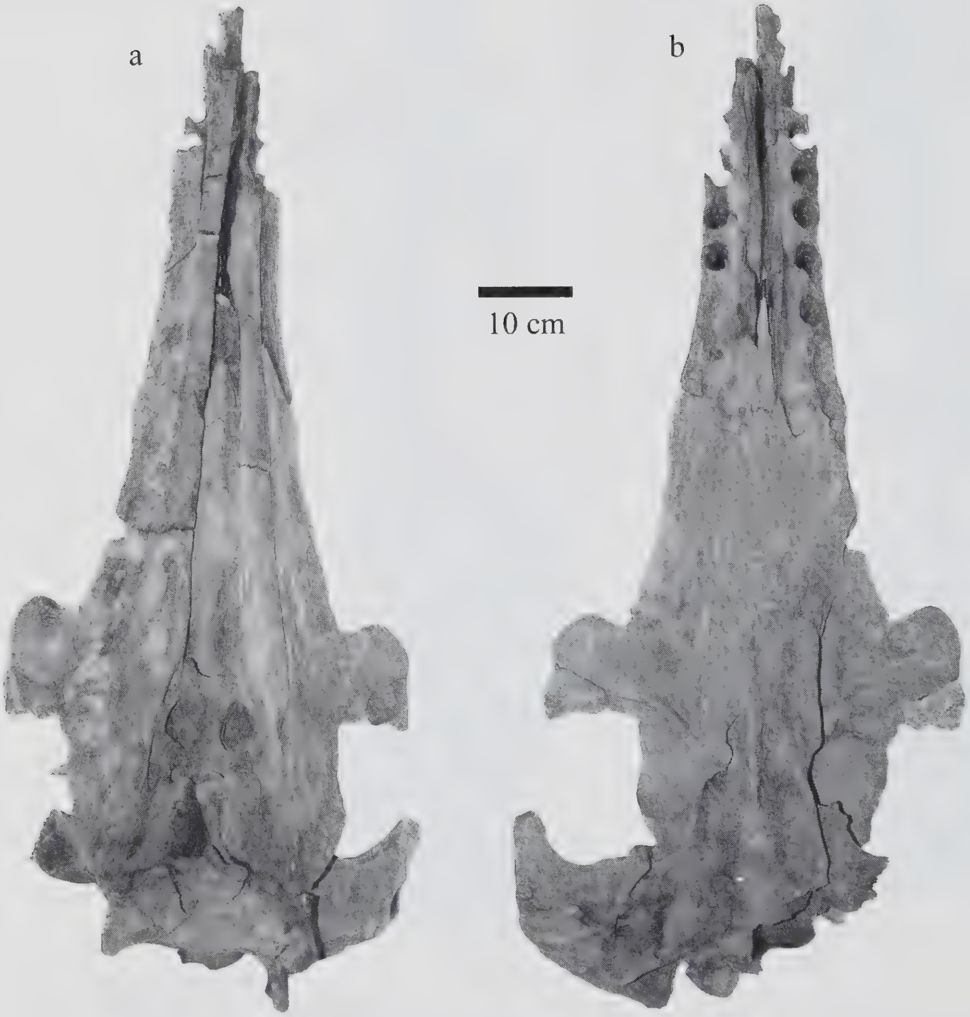

Figure 3.–*Squalodon whitmorei*, sp. nov., paratype cranium, USNM 424070. a, dorsal view; b, ventral view. Scale = 10 cm.

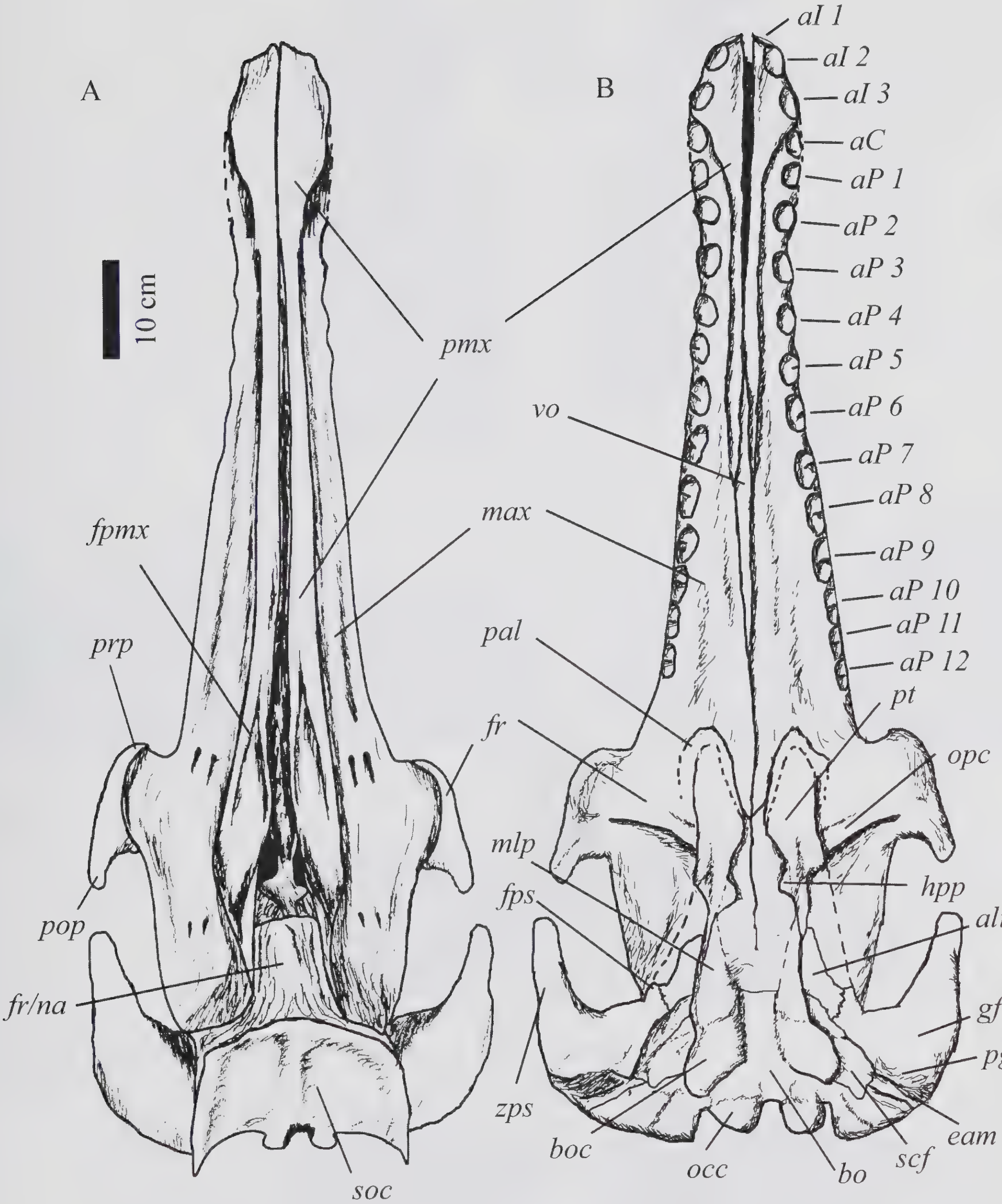

Figure 4.–*Squalodon whitmorei*, sp. nov., reconstructed cranium. a, dorsal; b, ventral. Scale = 10 cm. For abbreviations see p.6.

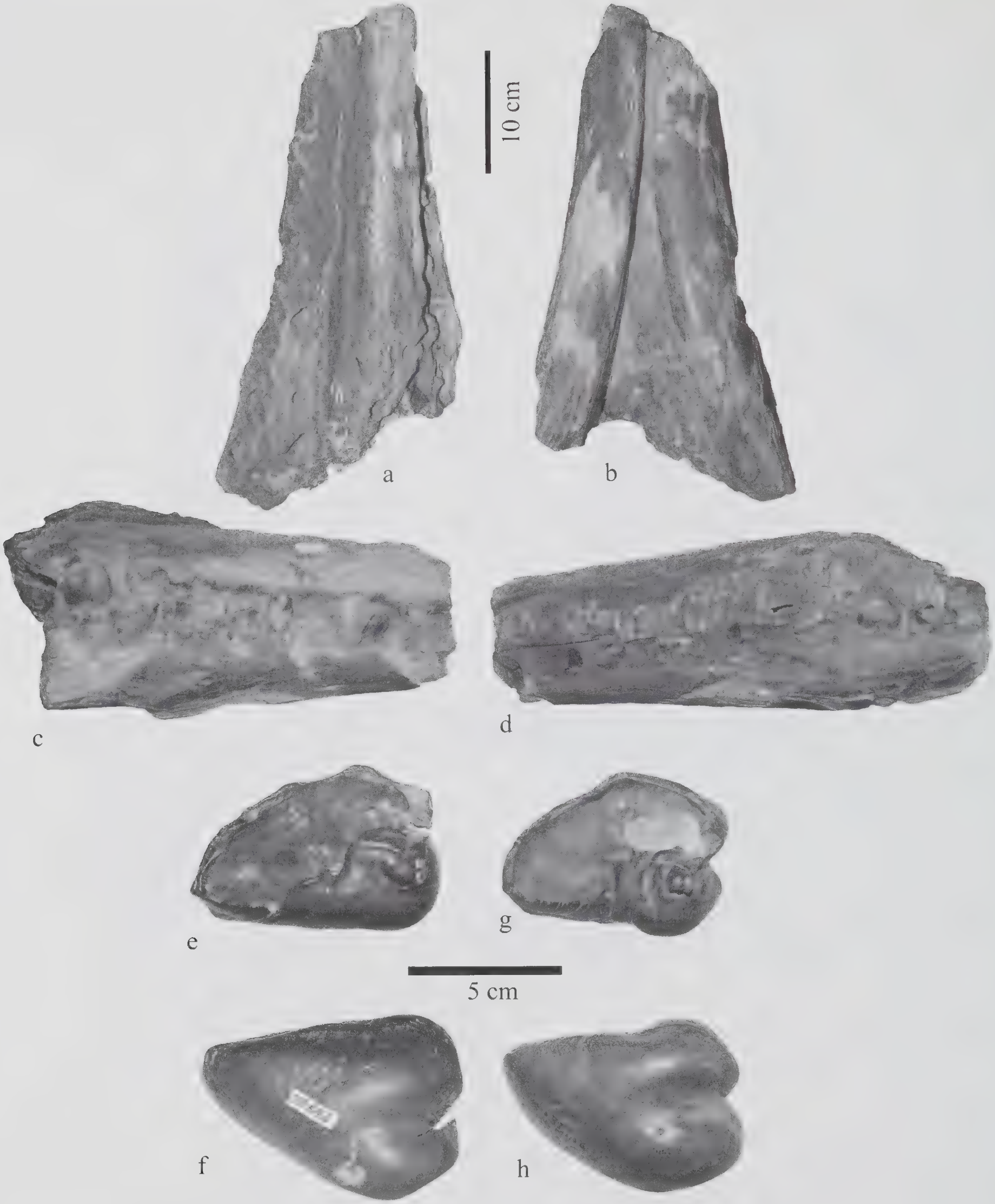

Figure 5.–*Squalodon whitmorei*, sp. nov., referred cranium and mandible fragment and tympanic bullae. a-d, USNM181575, cranium and mandible fragment. a, dorsal view; b, ventral view; c, right lateral view; d, left lateral view. e, f, USNM 181643, right tympanic bulla. e, dorsal view; f, lateral view. g, h, USNM 181644, right tympanic bulla. g, dorsal view; h, lateral view. Scale = 5 cm.

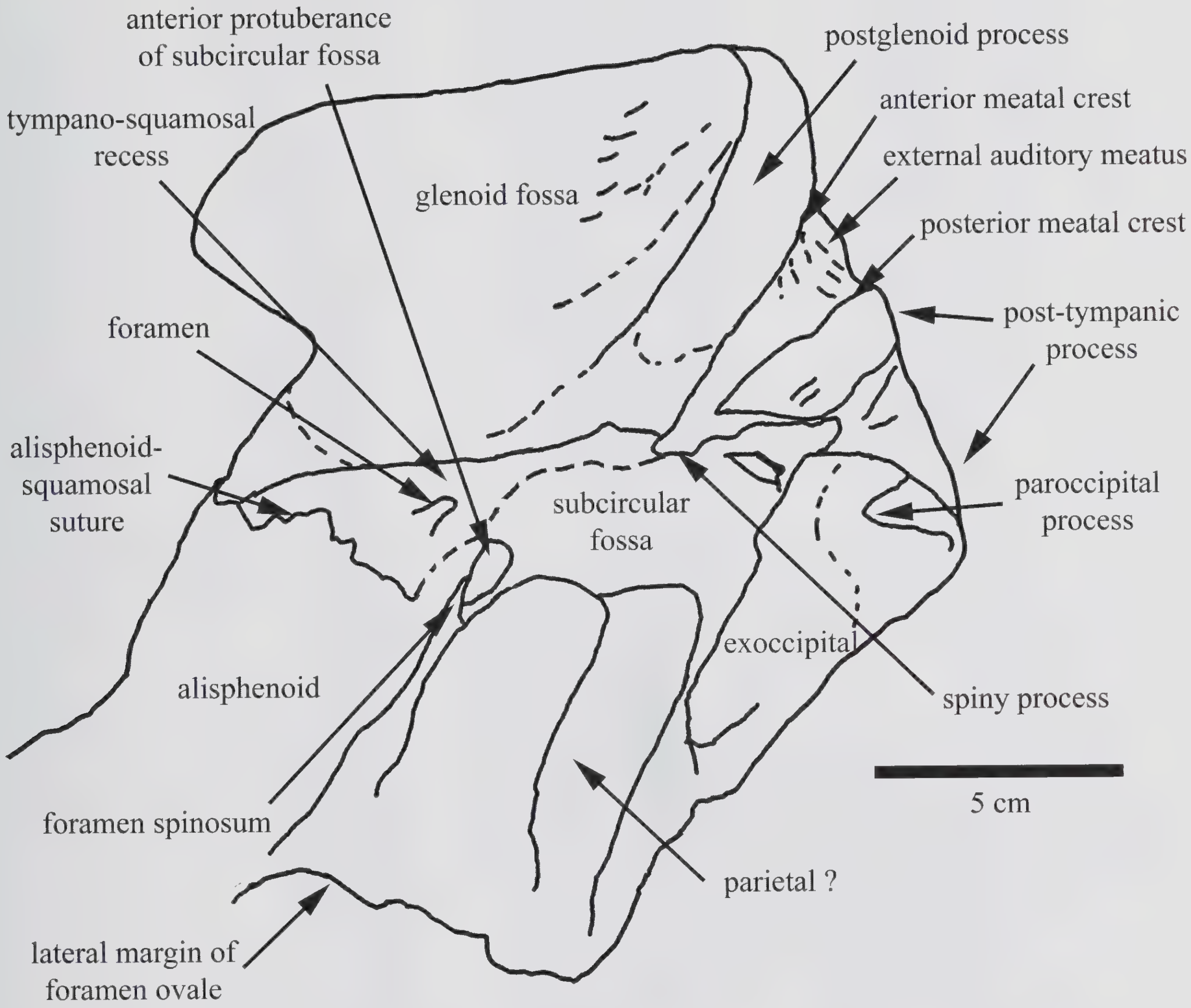

Figure 6.–Interpretation of the details of the basicranium of *Squalodon whitmorei*, sp. nov., based on USNM 183023. Left side, ventromedial view. Terminology is after Fordyce (1994).

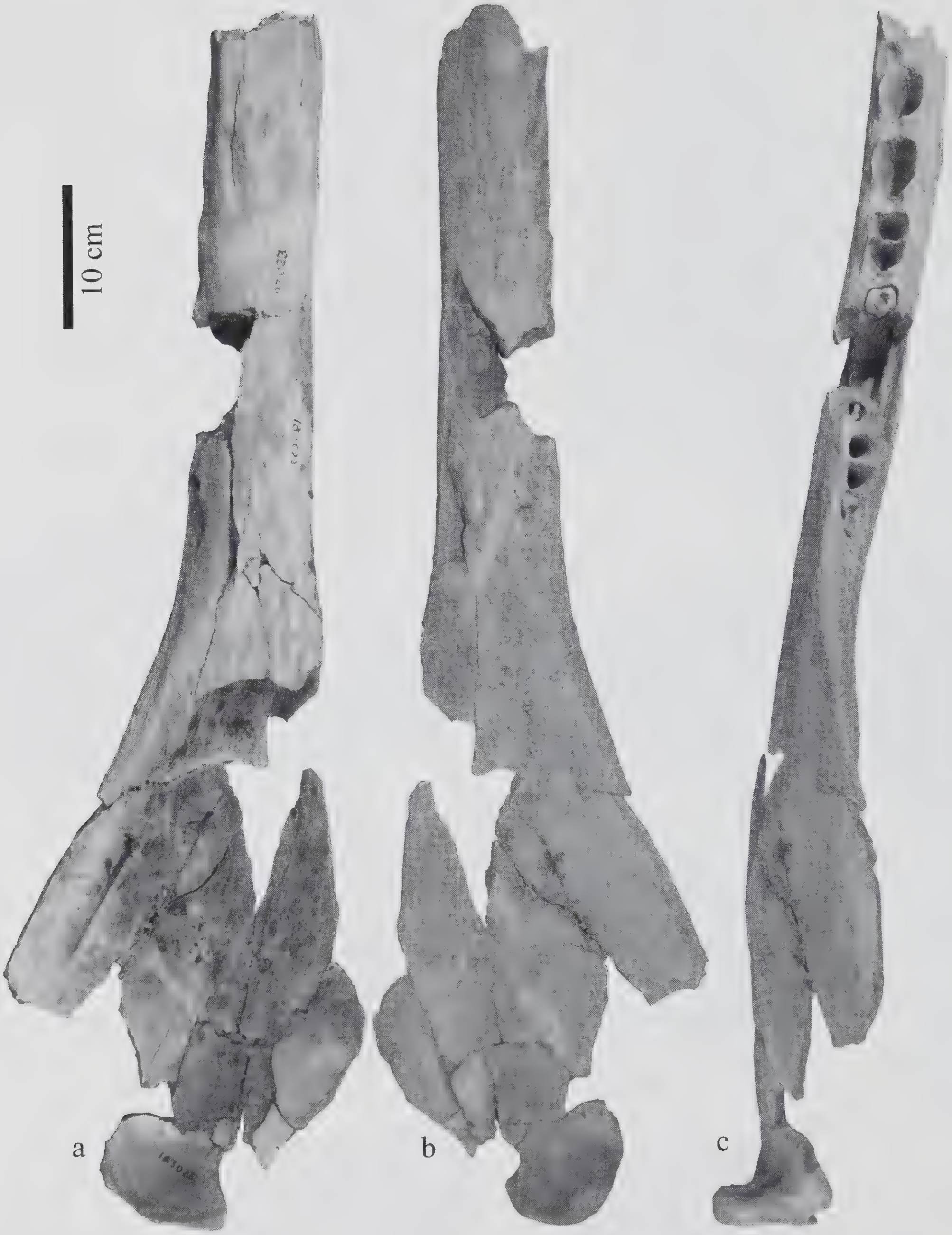

Figure 7.– *Squalodon whitmorei*, sp. nov., holotype left dentary, USNM 183023. a, medial view; b, lateral view; c, dorsal view. Scale = 10 cm.

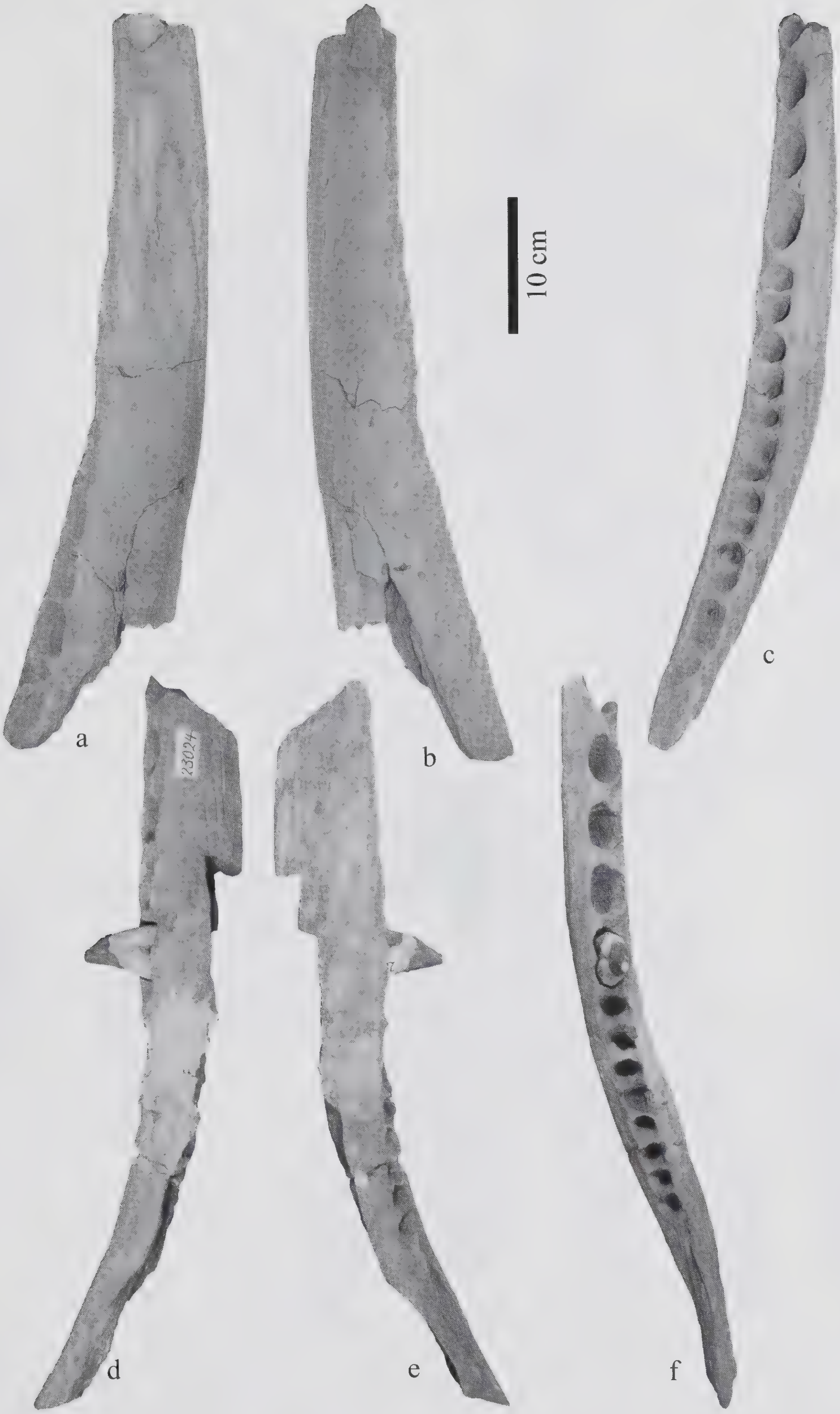

Figure 8.– *Squalodon whitmorei*, sp. nov., dentaries. a-c, CMM-V-182, left dentary. a, medial view; b, lateral view; c, dorsal view. d-f USNM 23024, right dentary. d, lateral view; e, medial view; f, dorsal view. Scale = 10 cm.

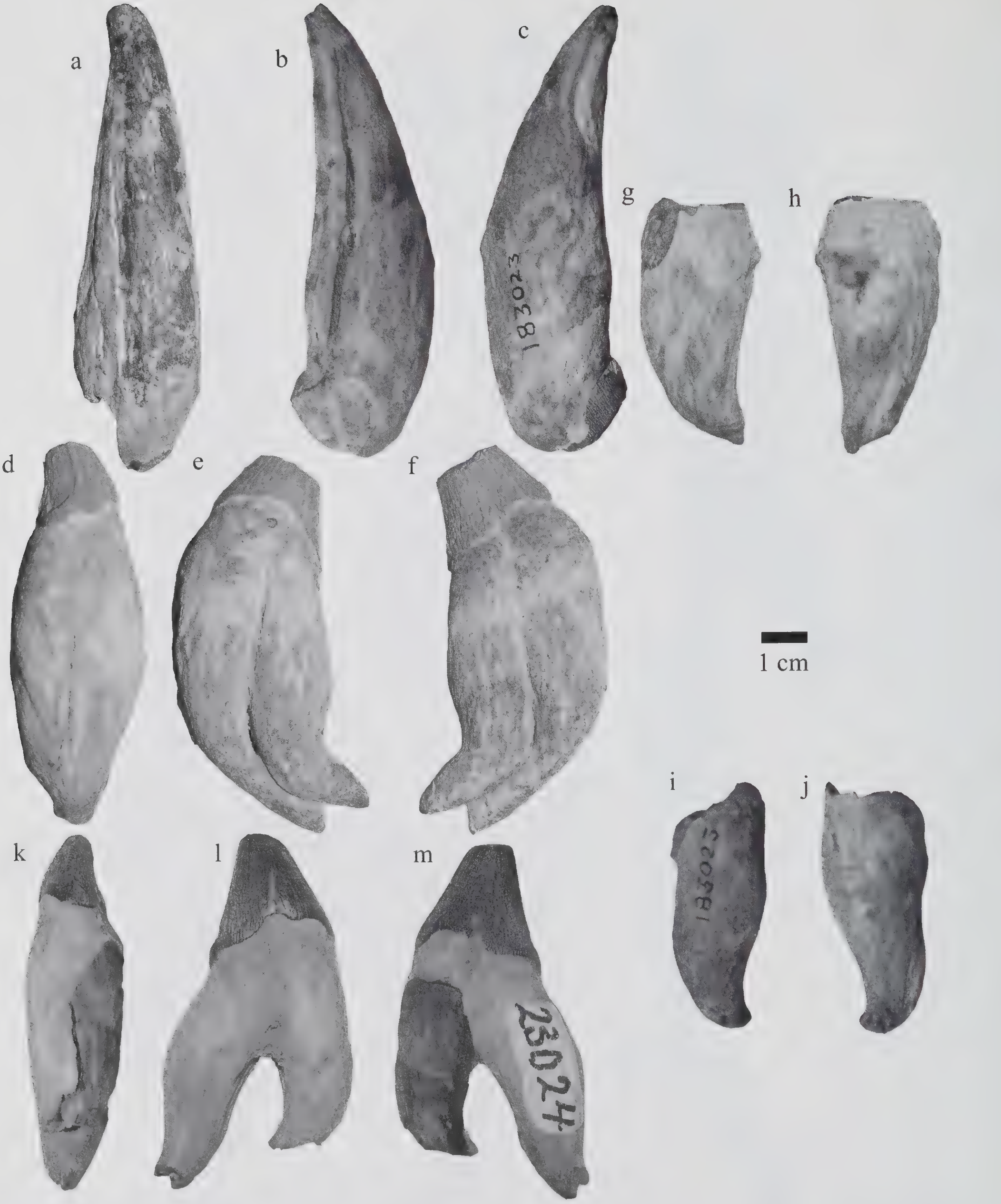

Figure 9.– *Squalodon whitmorei*. sp. nov., teeth. a-j, holotype, USNM 183023. a, upper left I1 medial; b, c, upper left canine, b, lateral view, c, medial view; d-f, sixth lower left cheek tooth, d, anterior view, e, lateral view, f, medial view; g-h, fifth lower left cheek tooth, posterior root; g, lateral view, h, medial view; i-j, fourth lower left cheek tooth, anterior root, i, lateral view, j, medial view. k-m, referred specimen, USNM 23024, fifth lower right cheek tooth, k, anterior view, l, lateral view, m, medial view. Scale = 1 cm.

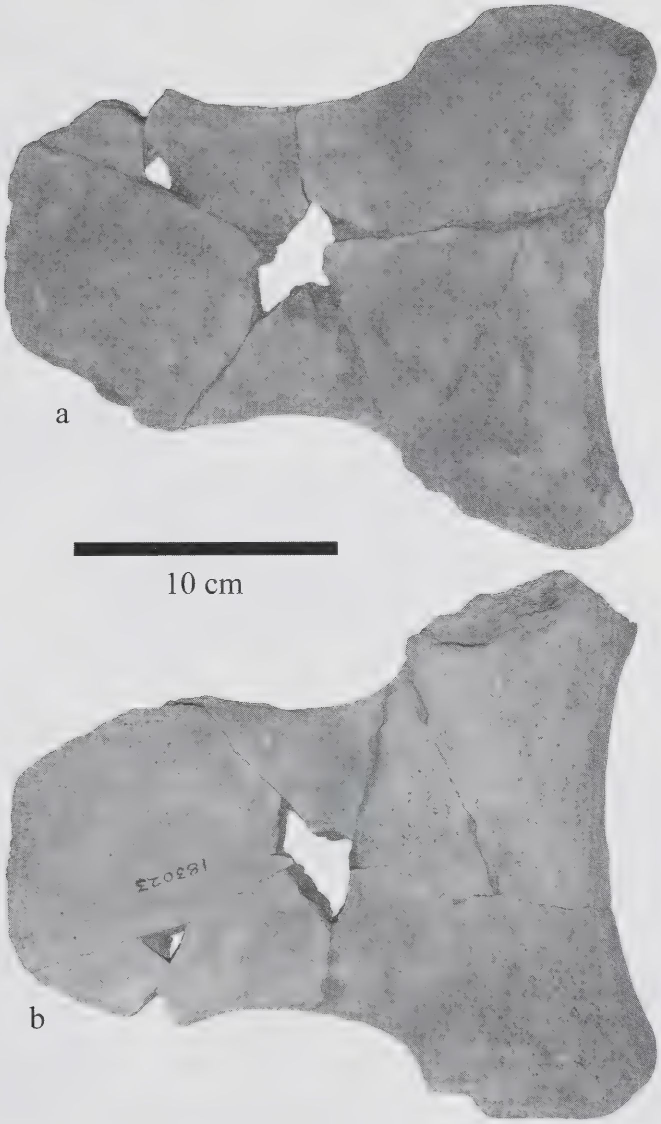

Figure 10.— *Squalodon whitmorei*, sp. nov., holotype manubrium, USNM 183023. a, ventral view; b, dorsal view. Scale = 10 cm.

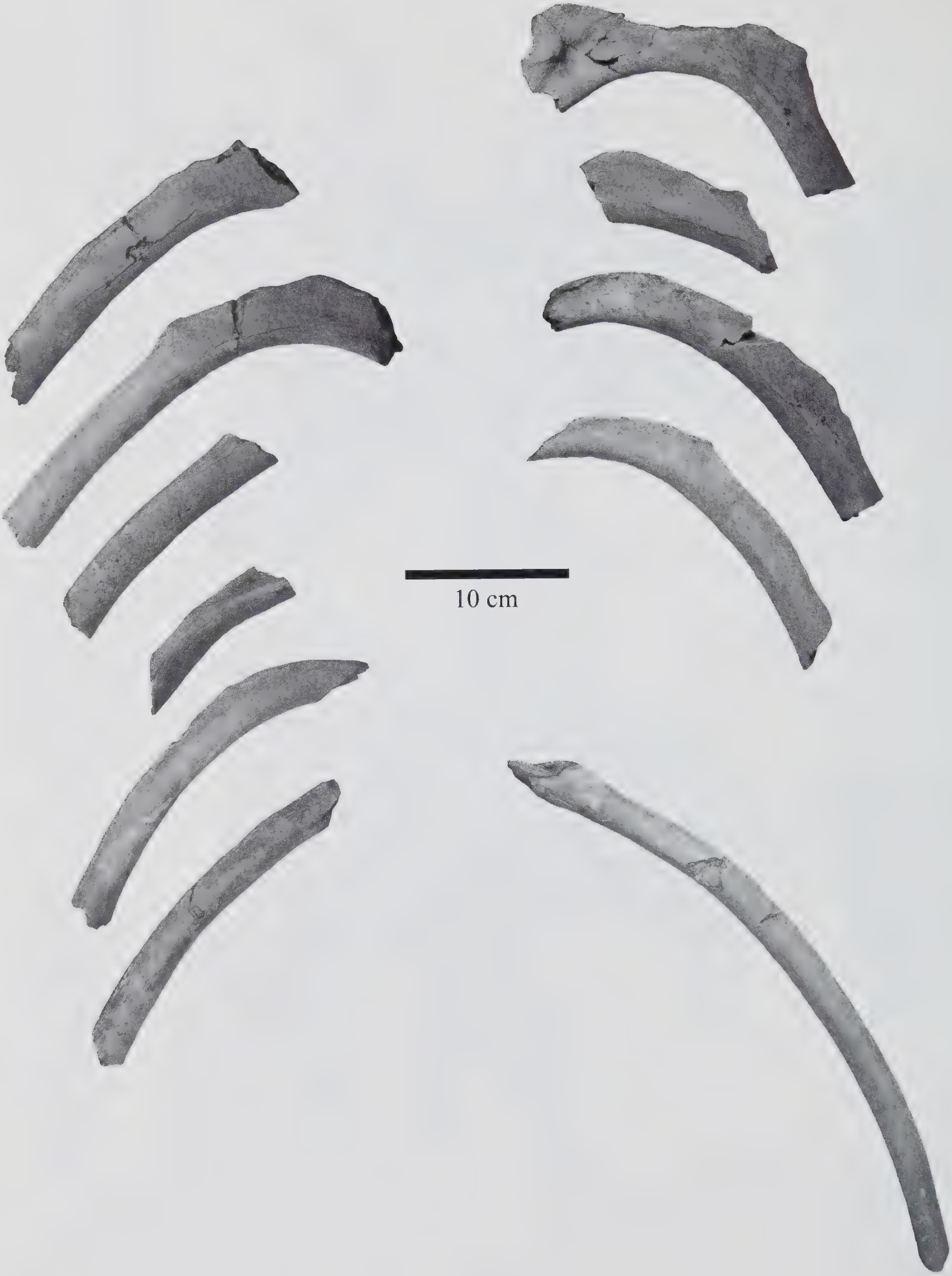

Figure 11.– *Squalodon whitmorei,* sp. nov., holotype ribs, USNM 183023, posterior view. Scale = 10 cm.

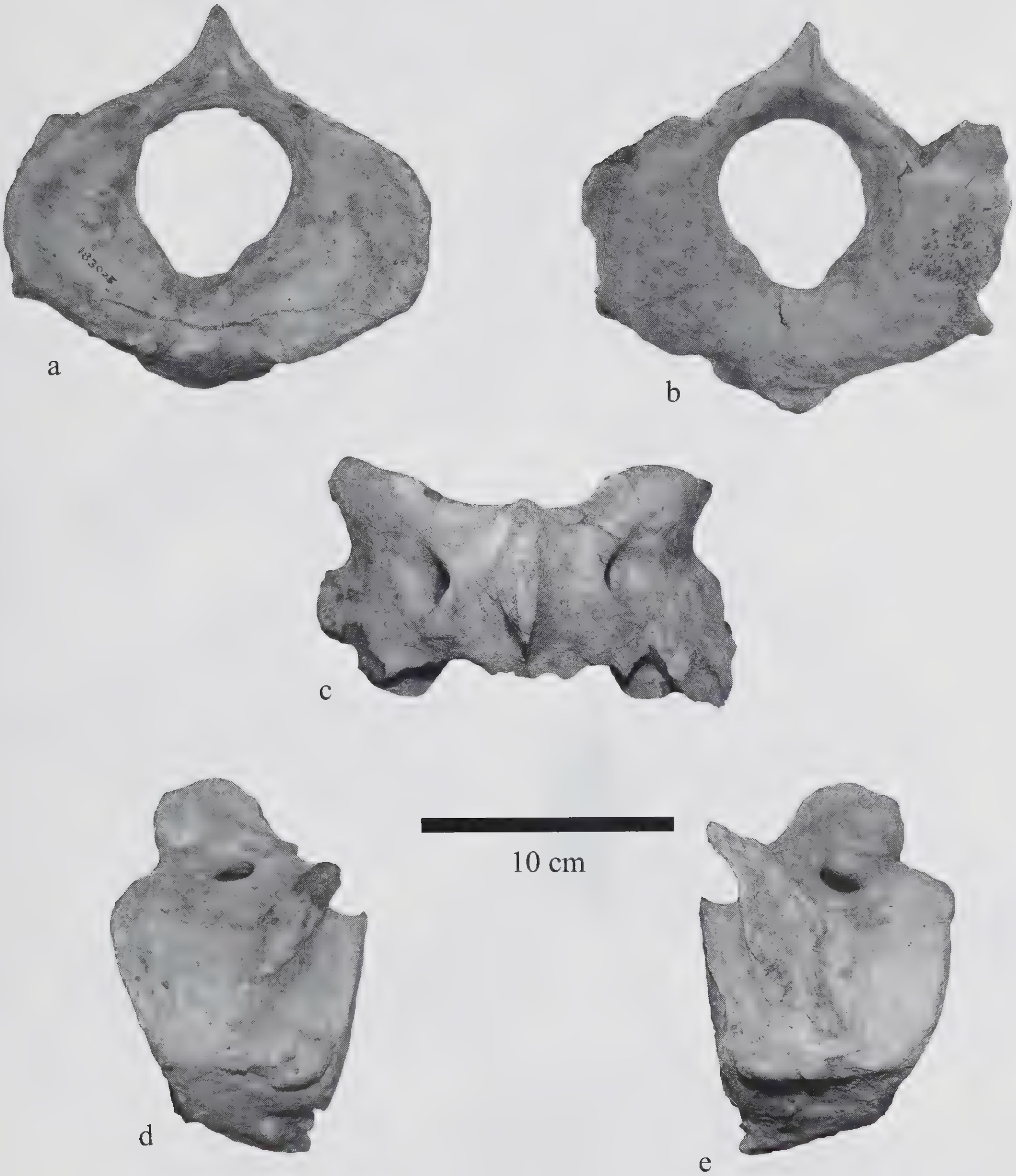

Figure 12.– *Squalodon whitmorei*, sp. nov., holotype atlas, USNM 183023. a, anterior view; b, posterior view; c, dorsal view; d, left lateral view; e, right lateral view. Scale = 10 cm.

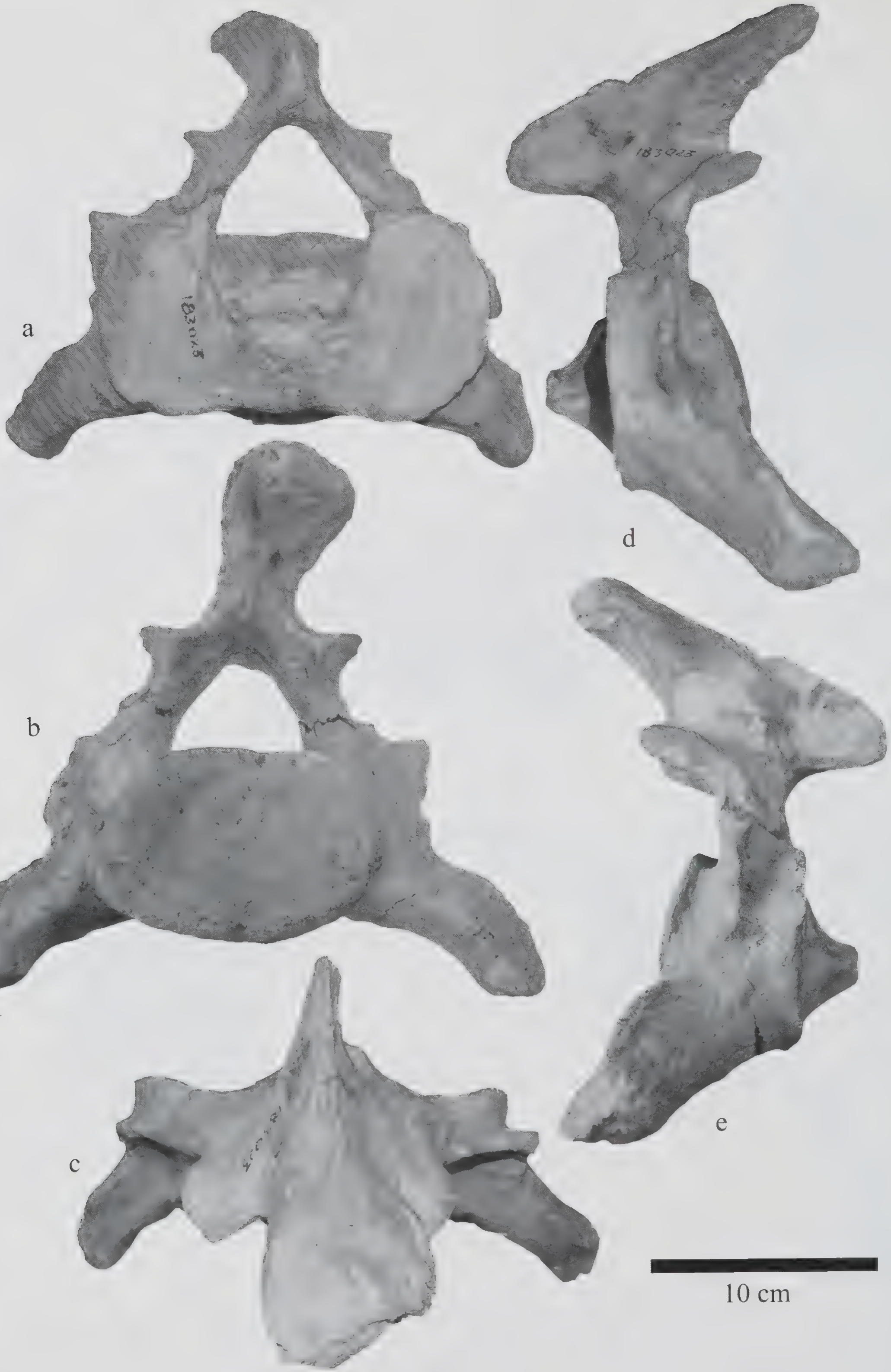

Figure 13.– *Squalodon whitmorei*, sp. nov., holotype axis, USNM 183023. a, anterior view; b, posterior view; c, dorsal view; d, left lateral view; e, right lateral view. Scale = 10 cm.

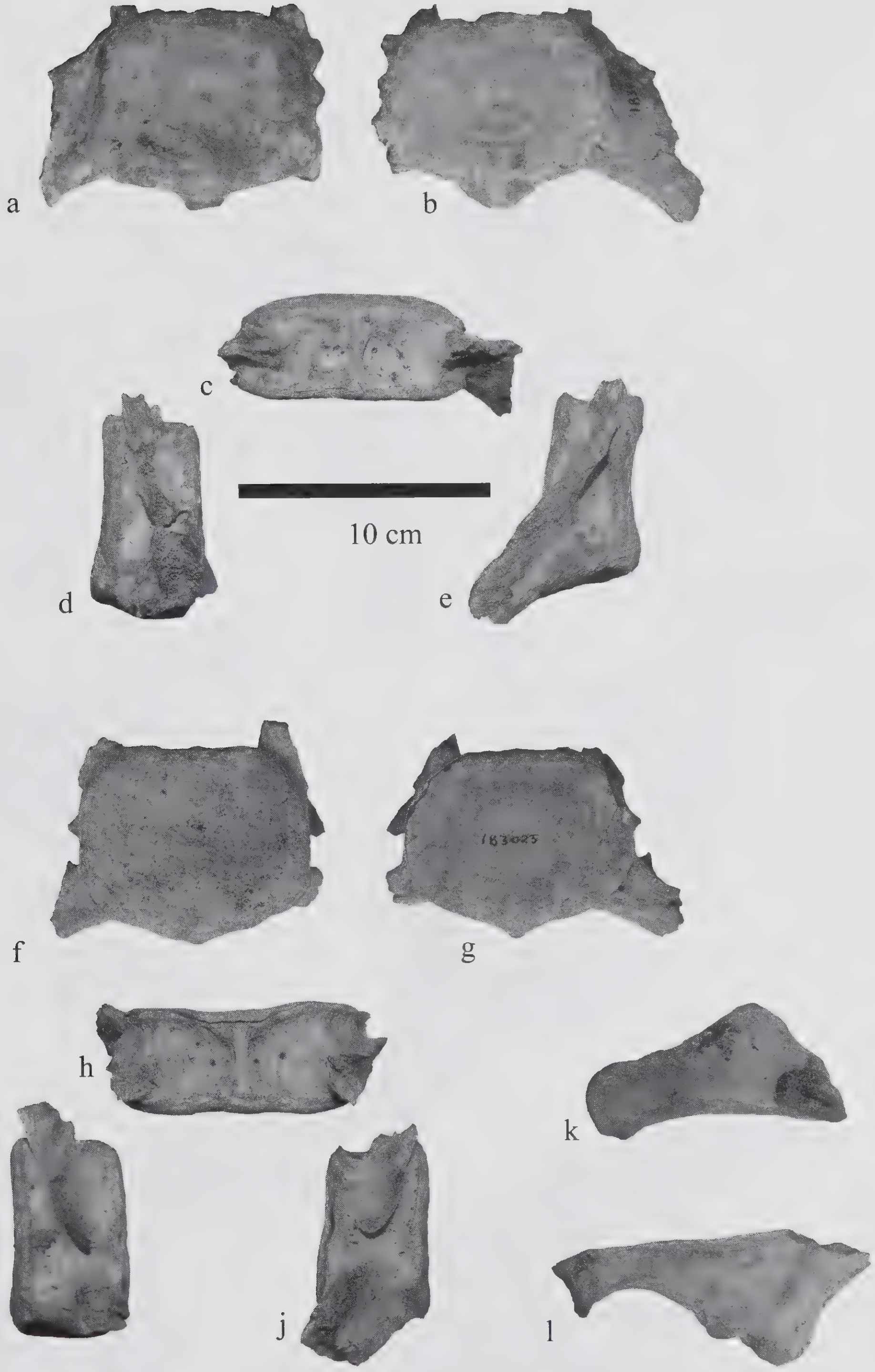

Figure 14.– *Squalodon whitmorei*, sp. nov., holotype cervical vertebrae 3-6, USNM 183023. a-e, Ce3. a, anterior view; b, posterior view; c, dorsal view; d, left lateral view; e, right lateral view. f-j, Ce4. f, anterior view; g, posterior view; h, dorsal view; i, left lateral view; j, right lateral view. k, Ce5, anterior view. l, Ce6, anterior view. Scale = 10 cm.

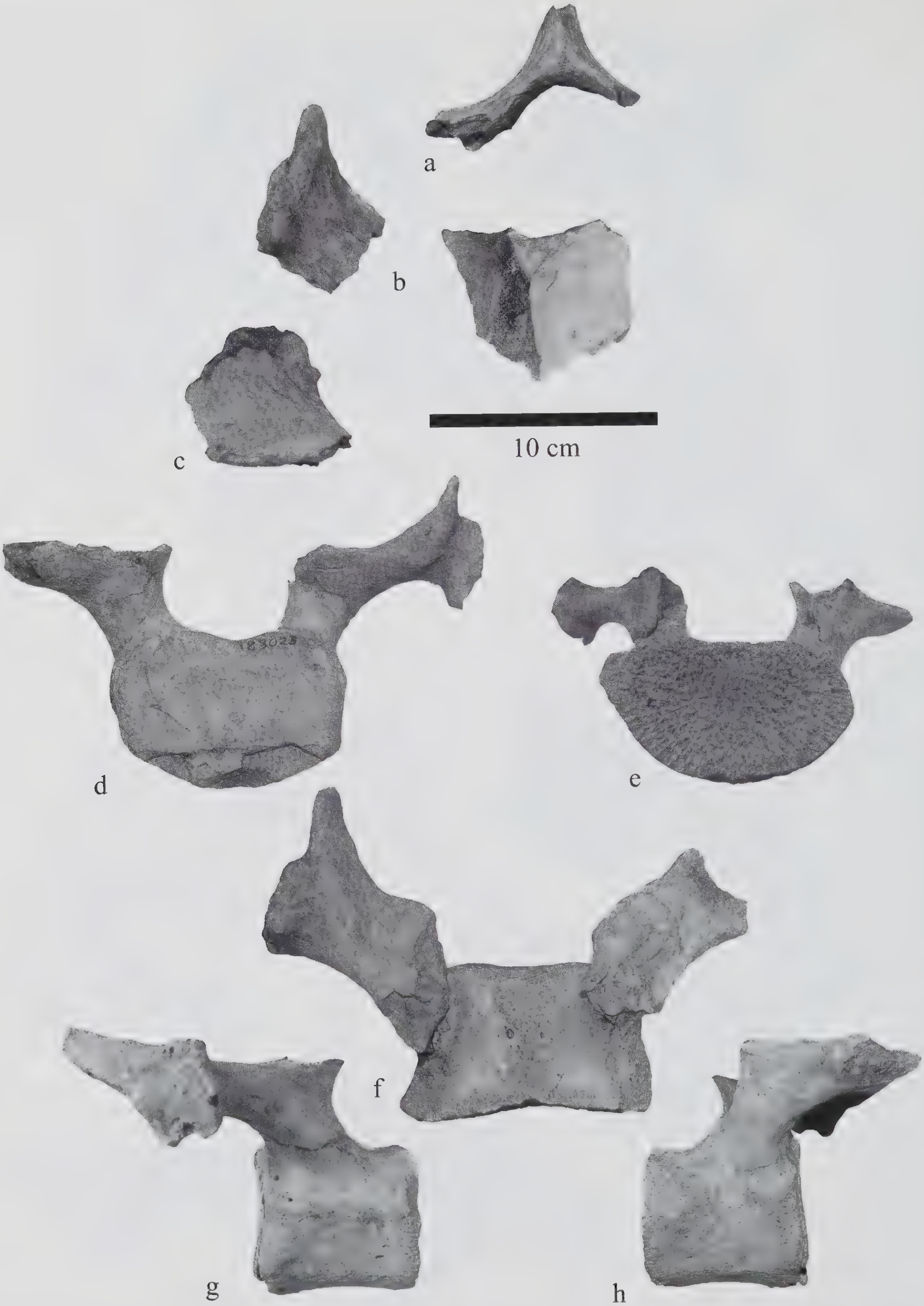

Figure 15.– *Squalodon whitmorei*, sp. nov., holotype thoracic vertebrae 1-2, USNM 183023. a-c, T1. a, anterior view; b, dorsal view; c, right lateral view. d-h, T2. d, anterior view; e, posterior view; f, dorsal view; g, left lateral view; h, right lateral view. Scale = 10 cm.

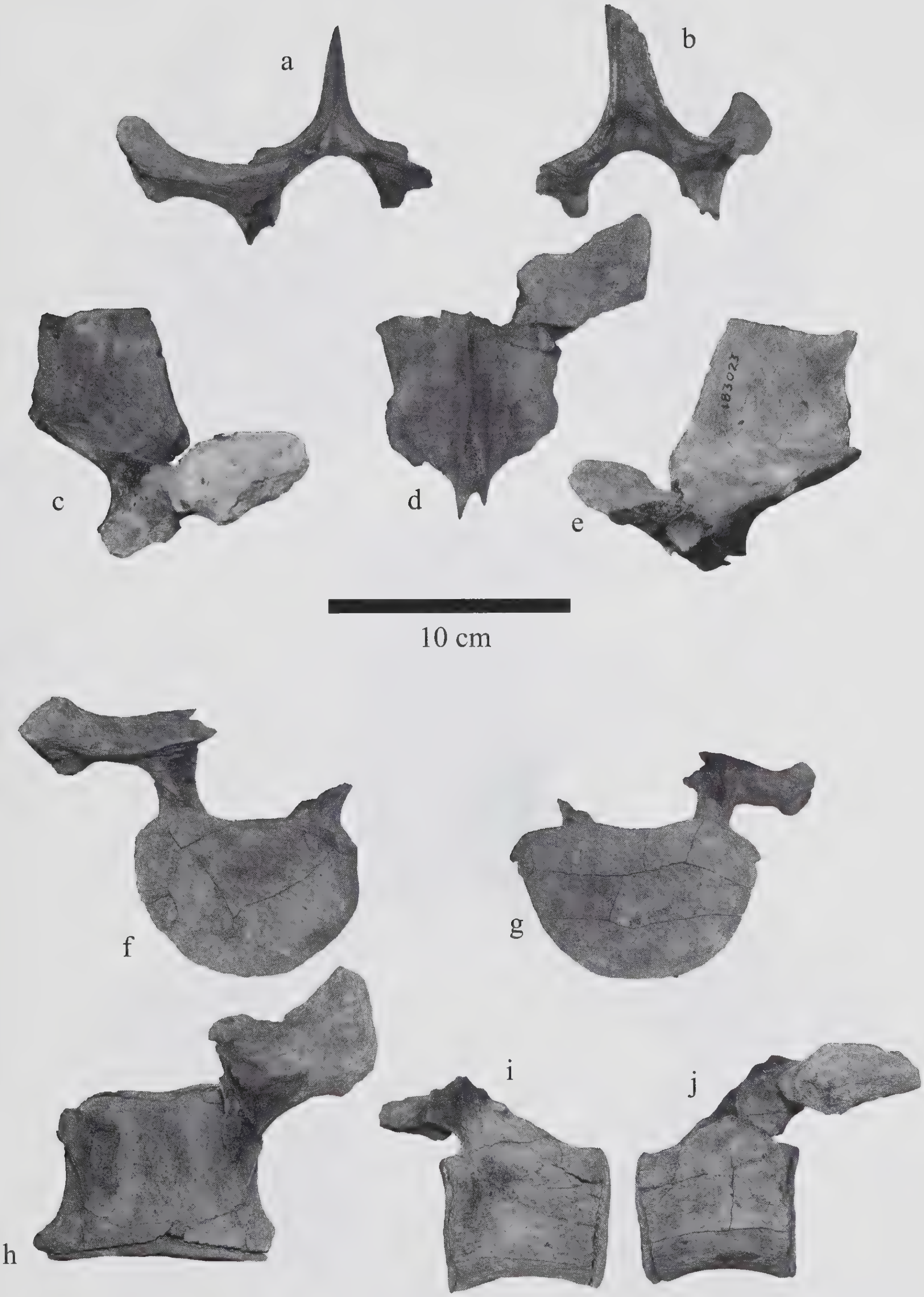

Figure 16.– *Squalodon whitmorei*, sp. nov., holotype thoracic vertebrae 3-4, USNM 183023. a-e, T3. a, anterior view; b, posterior view; c, right lateral view; d, dorsal view; e, left lateral view. f-j, T4. f, anterior view; g, posterior view; h, dorsal view; i, left lateral view; j, right lateral view. Scale = 10 cm.

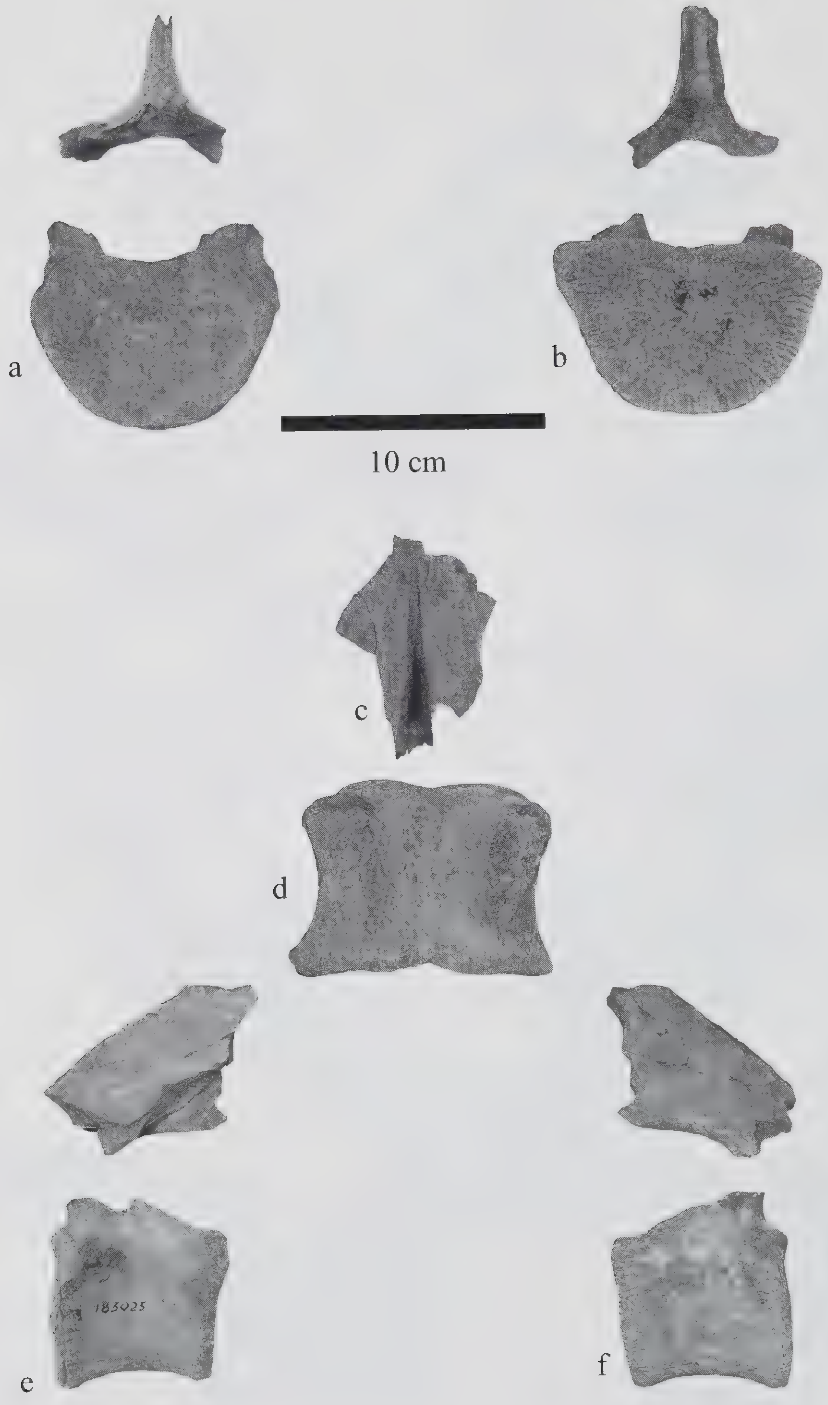

Figure 17.– *Squalodon whitmorei*, sp. nov., holotype thoracic vertebra 5, USNM 183023. a, anterior view; b, posterior view; c, dorsal view of neural spine; d, dorsal view of centrum; e, left lateral view; f, right lateral view. Scale = 10 cm.

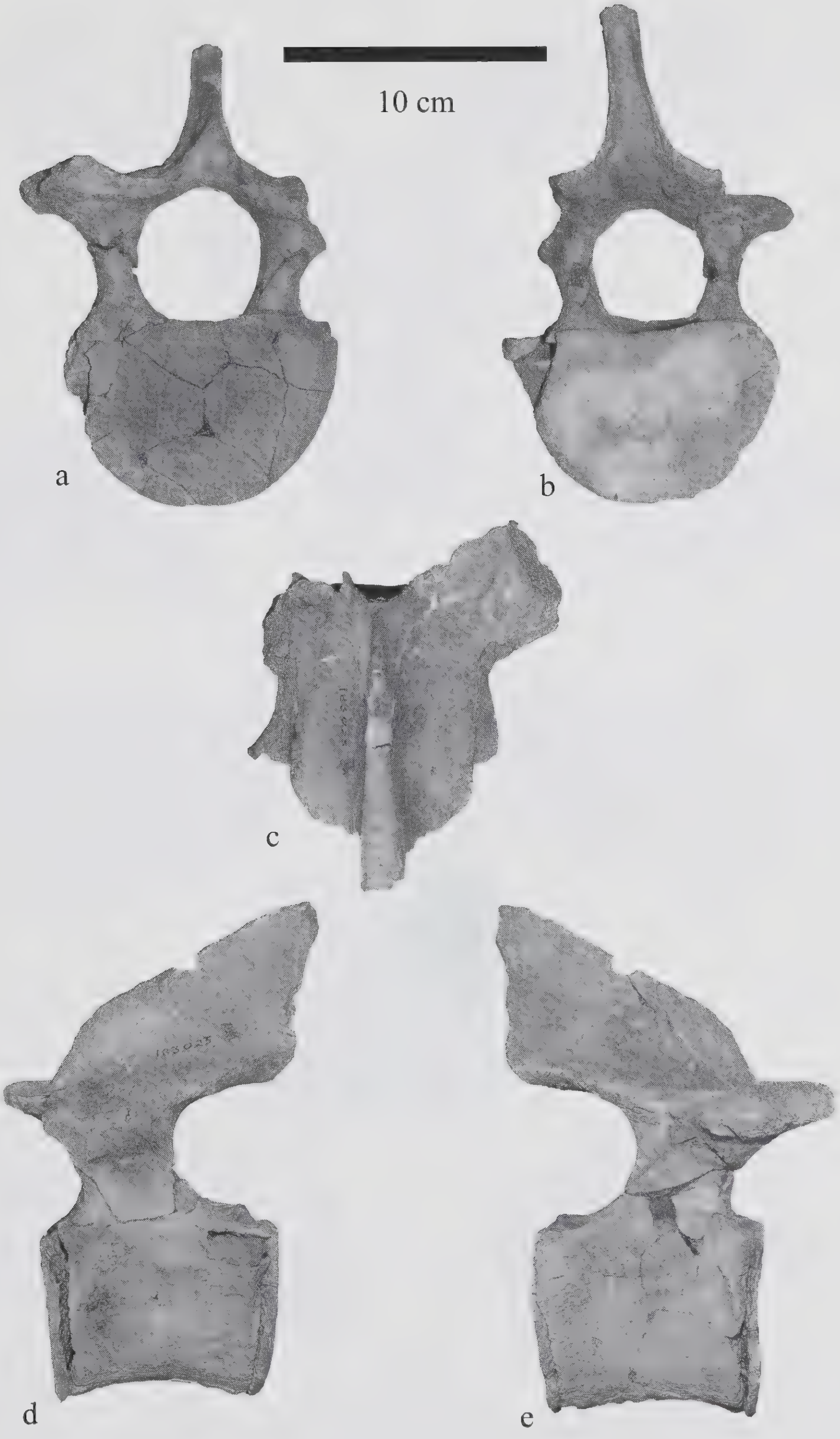

Figure 18.– *Squalodon whitmorei*, sp. nov., holotype thoracic vertebra 6, USNM 183023. a, anterior view; b, posterior view; c, dorsal view; d, left lateral view; e, right lateral view. Scale = 10 cm.

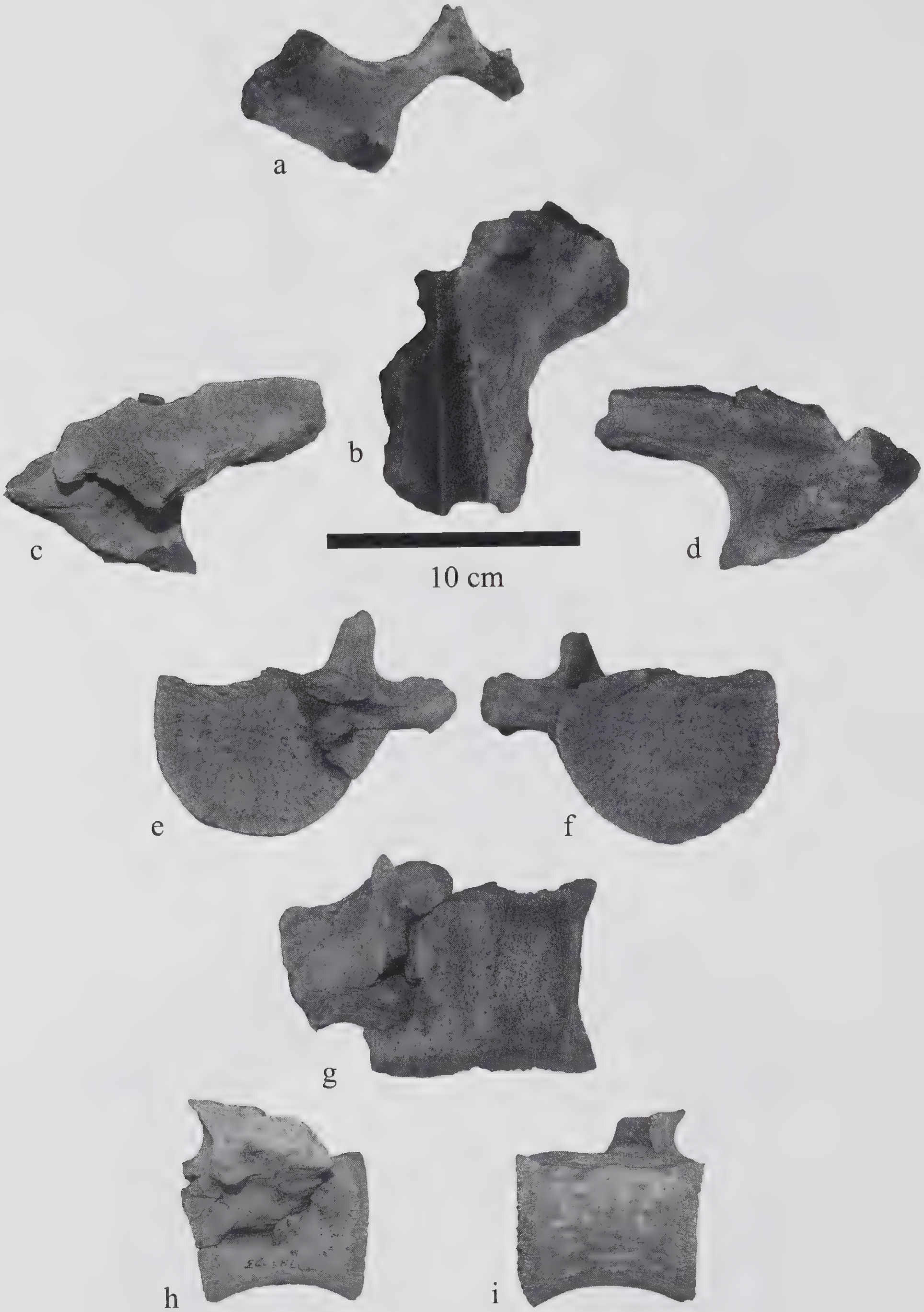

Figure 19.– *Squalodon whitmorei*, sp. nov., holotype thoracic vertebrae 7-8, USNM 183023. a-d, T7. a, anterior view; b, dorsal view; c, left lateral view; d, right lateral view. e-i, T8. e, anterior view; g, posterior view; h, dorsal view; i, left lateral view; j, right lateral view. Scale = 10 cm.

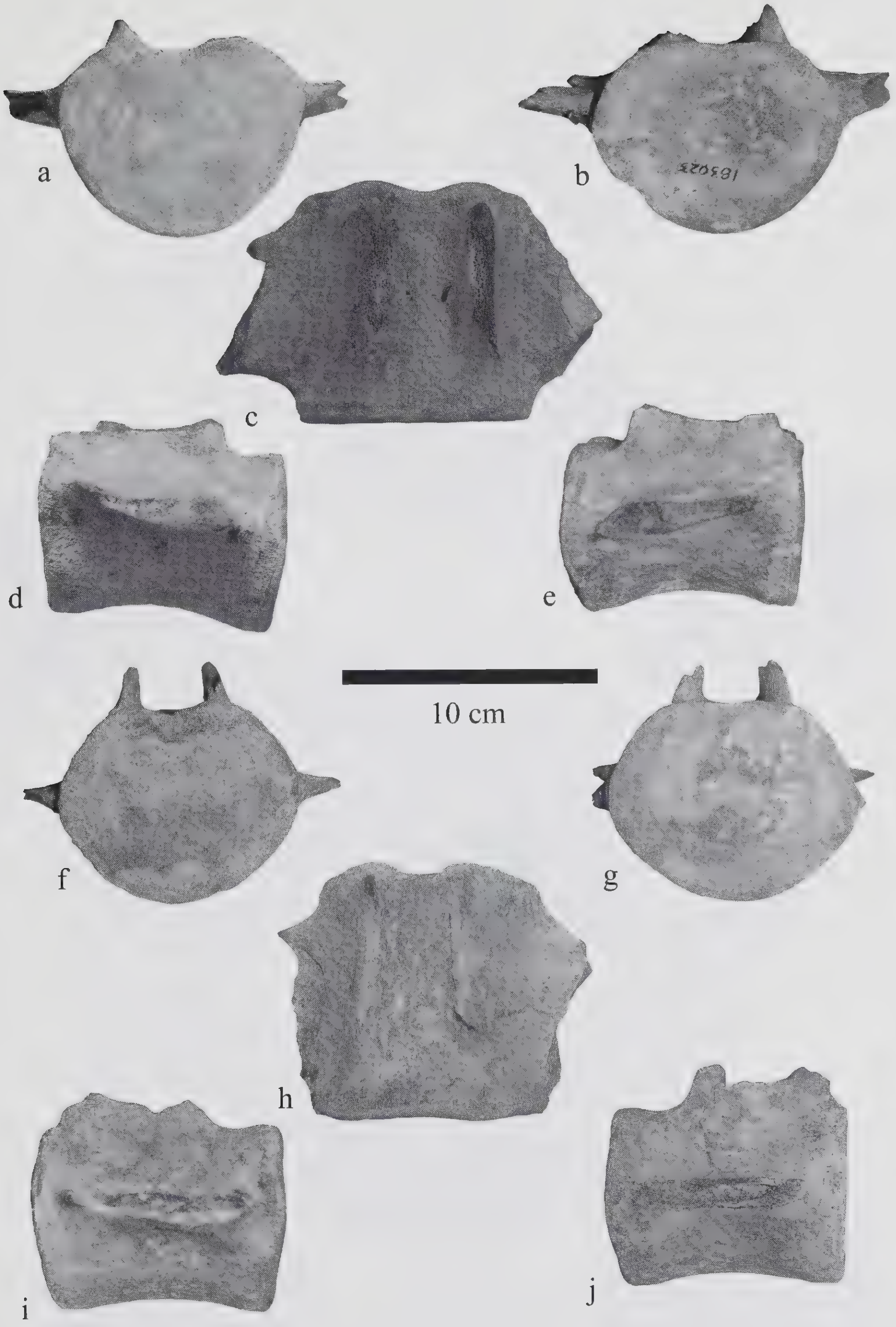

Figure 20.— *Squalodon whitmorei*, sp. nov., holotype thoracic vertebrae 9-10, USNM 183023. a-e, T9. a, anterior view; b, posterior view; c, dorsal view; d, left lateral view; e, right lateral view. f-j, T10. f, anterior view; g, posterior view; h, dorsal view; i, left lateral view; j, right lateral view. Scale = 10 cm.

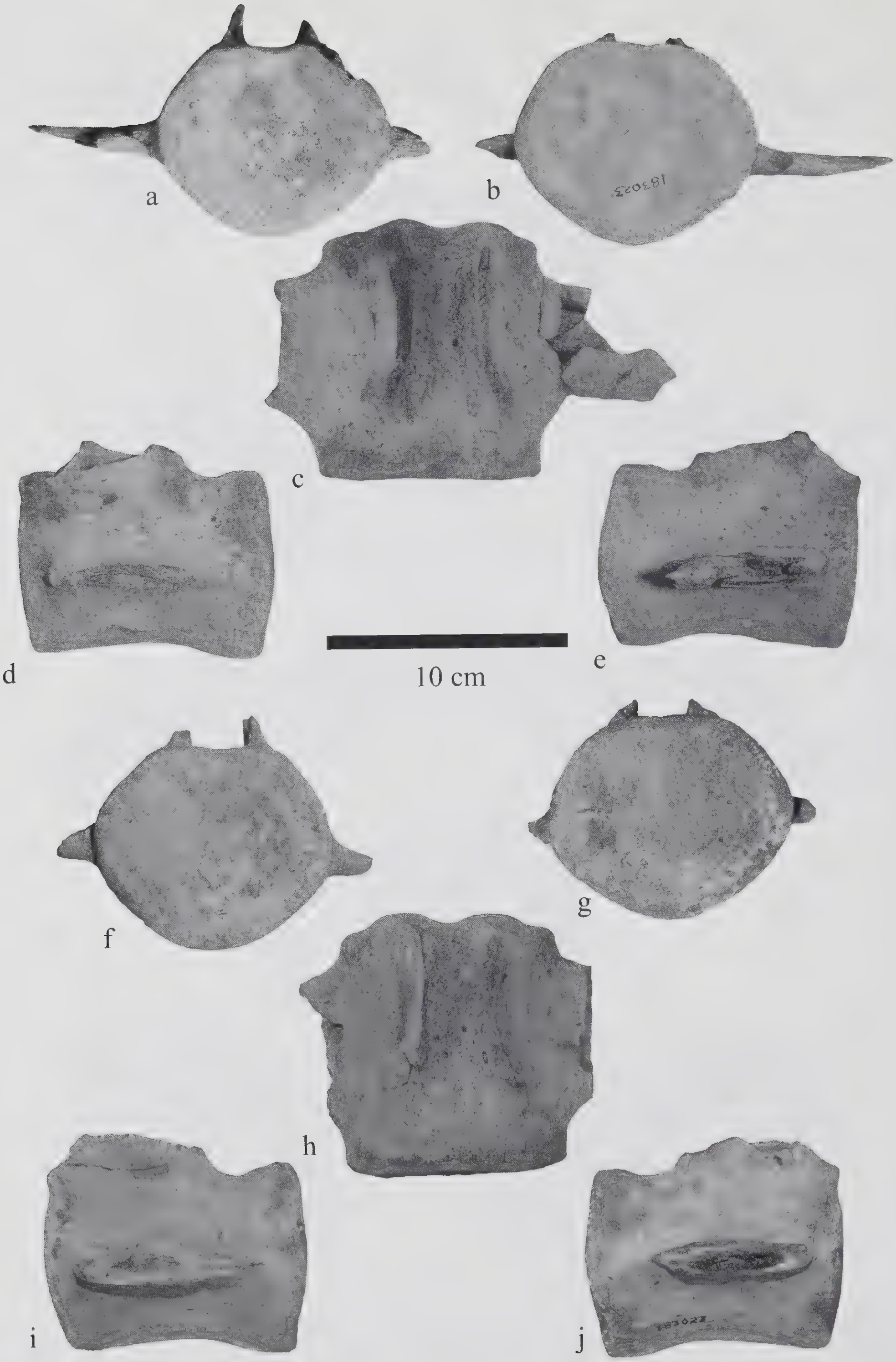

Figure 21.– *Squalodon whitmorei*, sp. nov., holotype thoracic vertebra 11 and lumbar vertebra 1, USNM 183023. a-e, T11. a, anterior view; b, posterior view; c, dorsal view; d, left lateral view; e, right lateral view. f-j, L1. f, anterior view; g, posterior view; h, dorsal view; i, left lateral view; j, right lateral view. Scale = 10 cm.

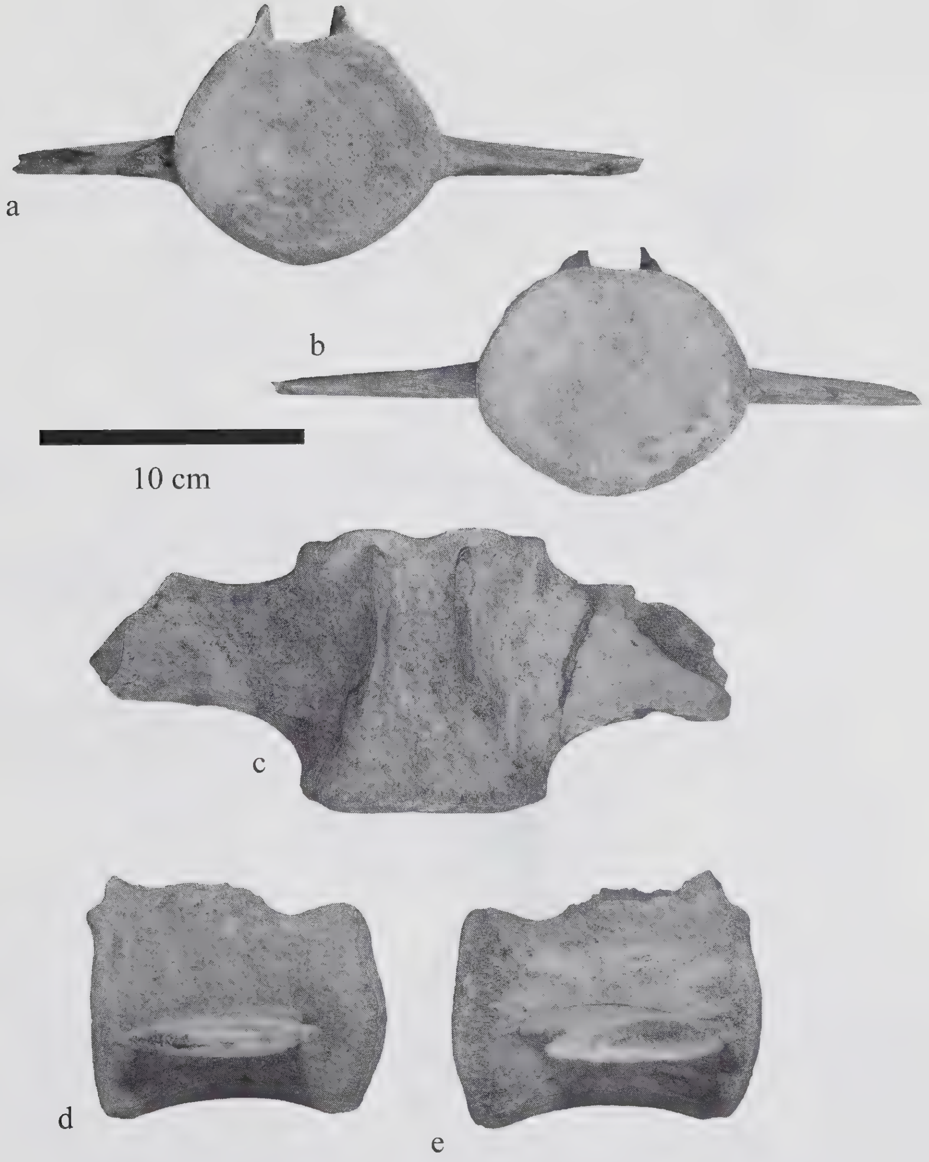

Figure 22.— *Squalodon whitmorei*, sp. nov., holotype lumbar vertebra 2, USNM 183023. a, anterior view; b, posterior view; c, dorsal view; d, left lateral view; e, right lateral view. Scale = 10 cm.

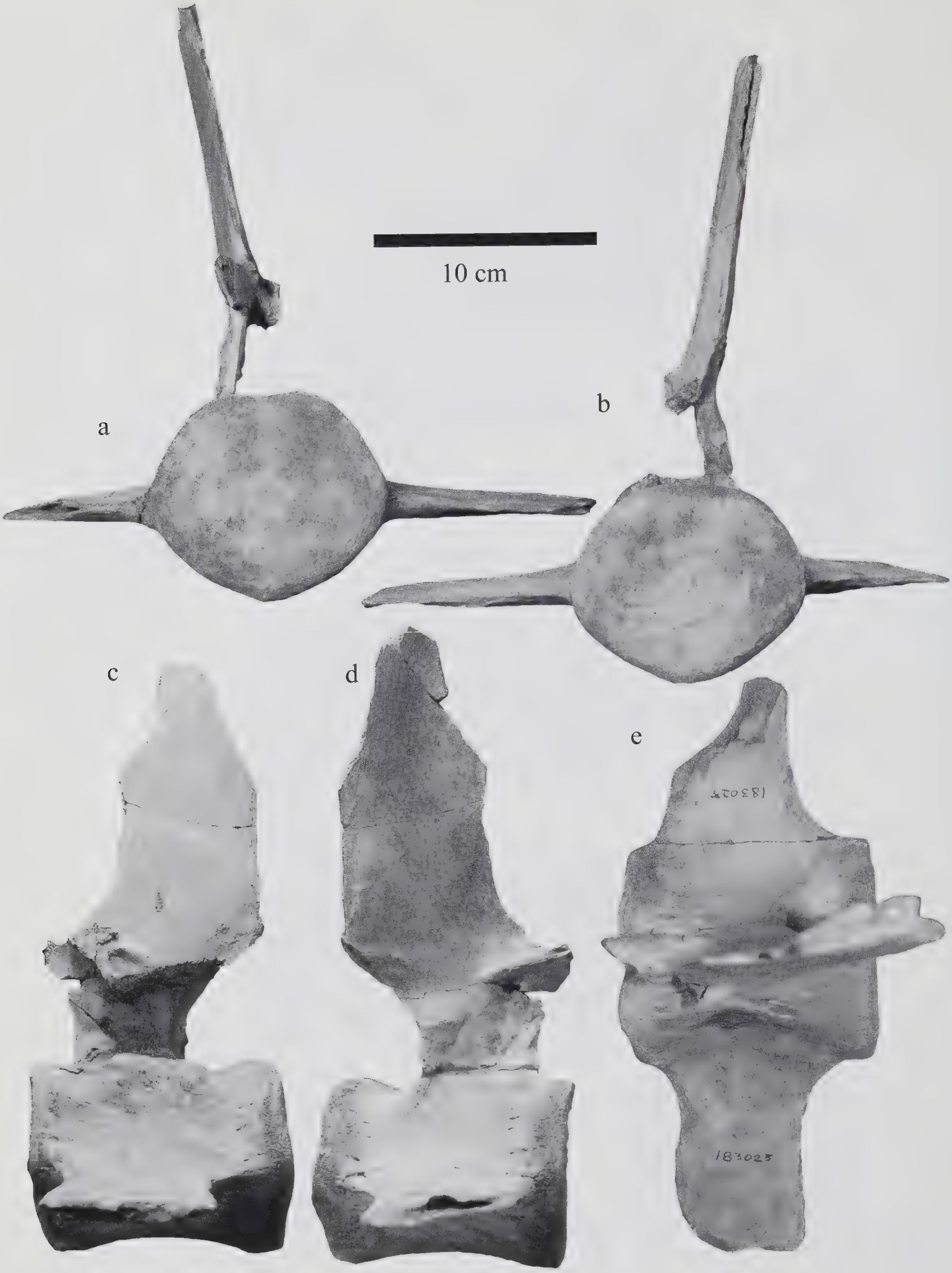

Figure 23.– *Squalodon whitmorei*, sp. nov., holotype lumbar vertebra 3, USNM 183023,. a, anterior view; b, posterior view; c, left lateral view; d, right lateral view; e, dorsal view. Scale = 10 cm.

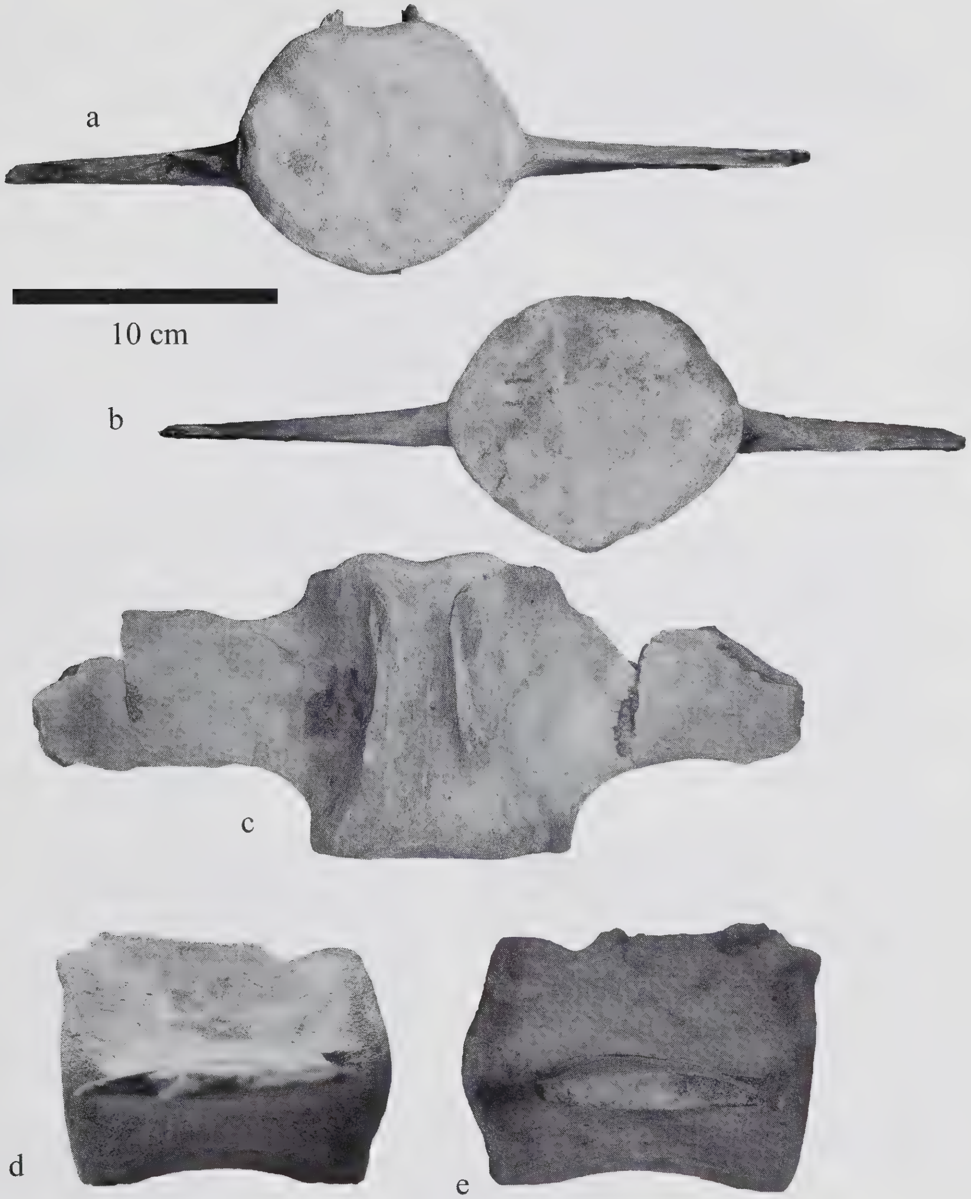

Figure 24.– *Squalodon whitmorei*, sp. nov., holotype lumbar vertebra 4, USNM 183023. a, anterior view; b, posterior view; c, dorsal view; d, left lateral view; e, right lateral view. Scale = 10 cm.

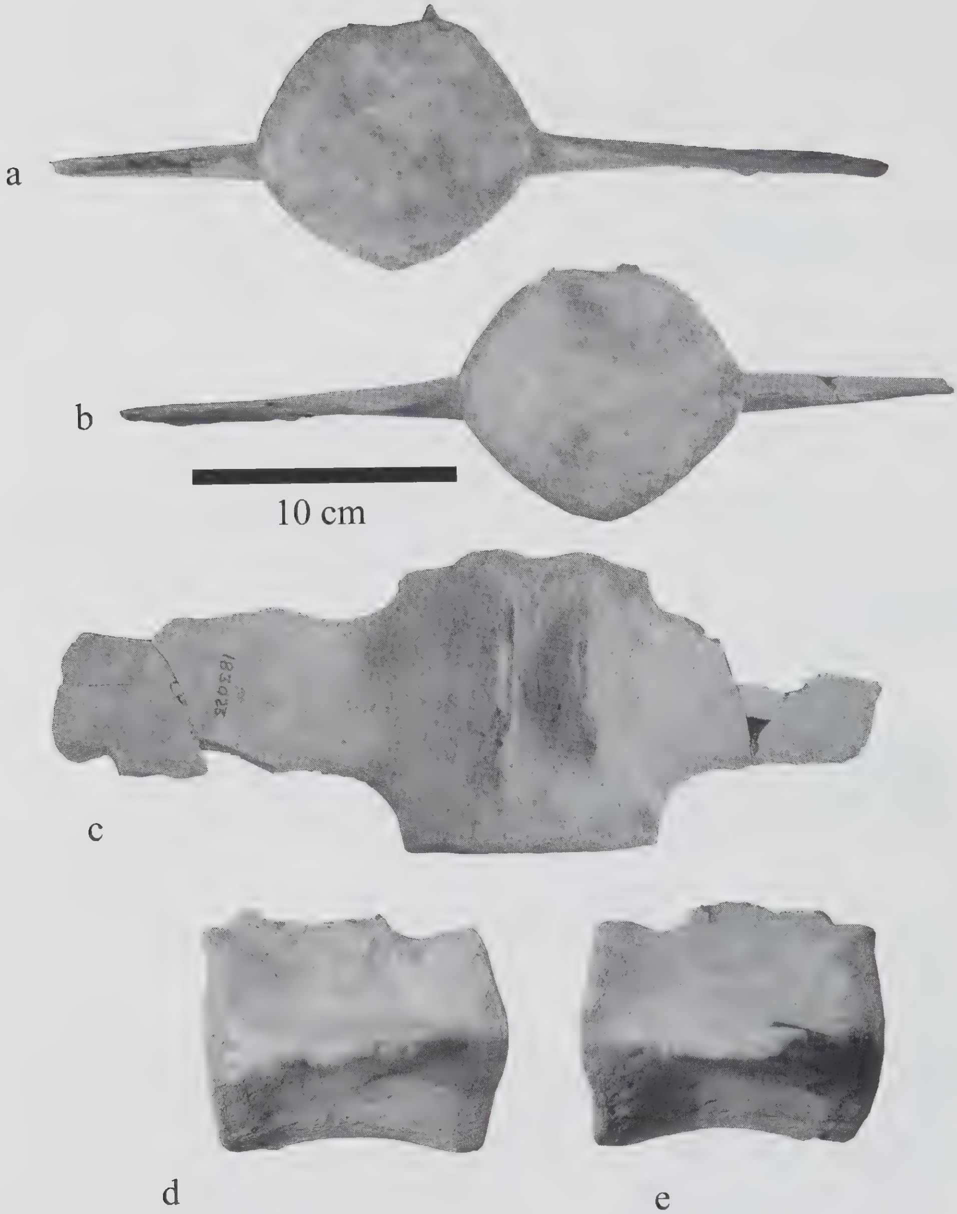

Figure 25.— *Squalodon whitmorei*, sp. nov., holotype lumbar vertebra 5, USNM 183023,. a, anterior view; b, posterior view; c, dorsal view; d, left lateral view; e, right lateral view. Scale = 10 cm.

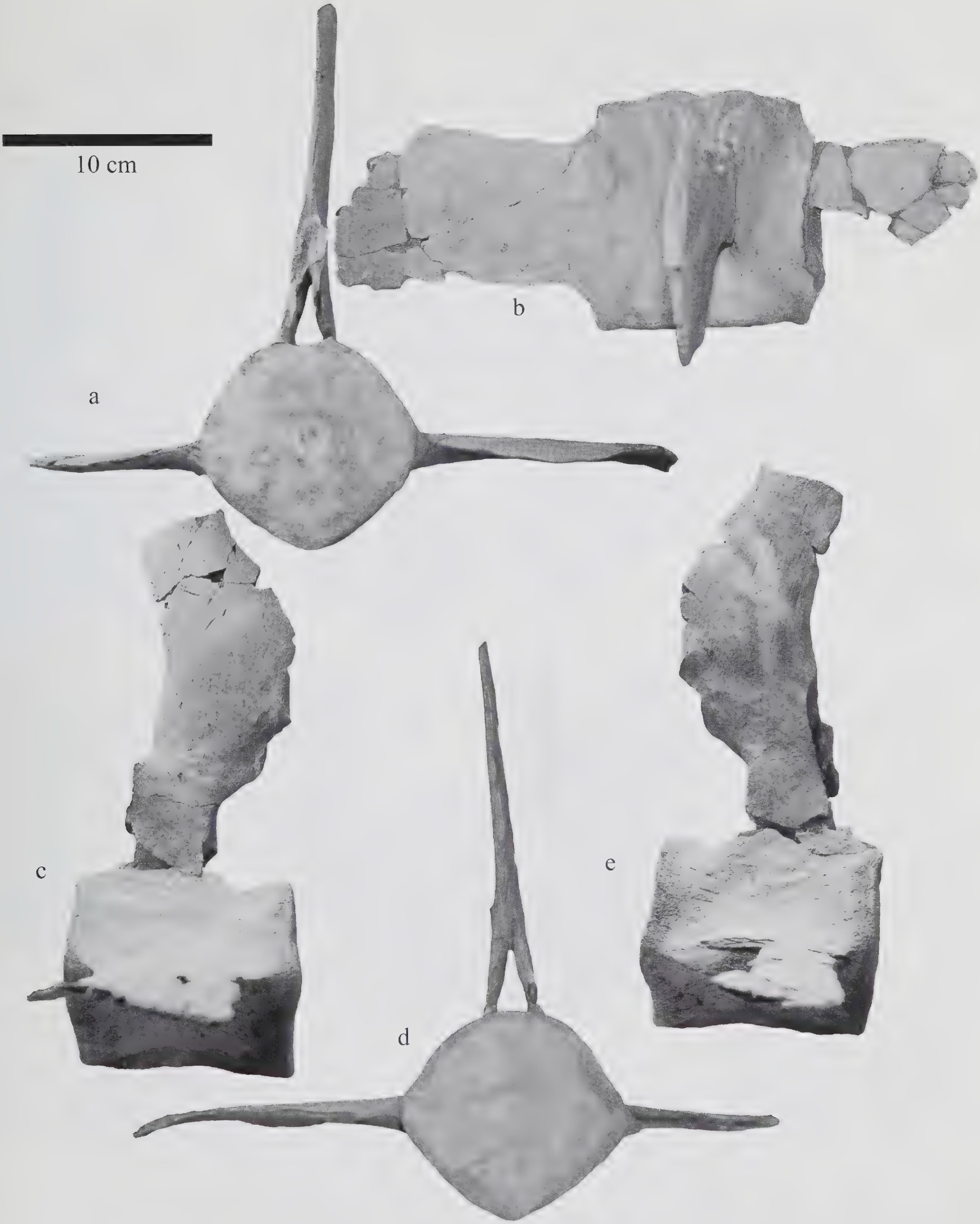

Figure 26.— *Squalodon whitmorei*, sp. nov., holotype lumbar vertebra 6, USNM 183023. a, anterior view; b, dorsal view; c, left lateral view; d, posterior view; e, right lateral view. Scale = 10 cm.

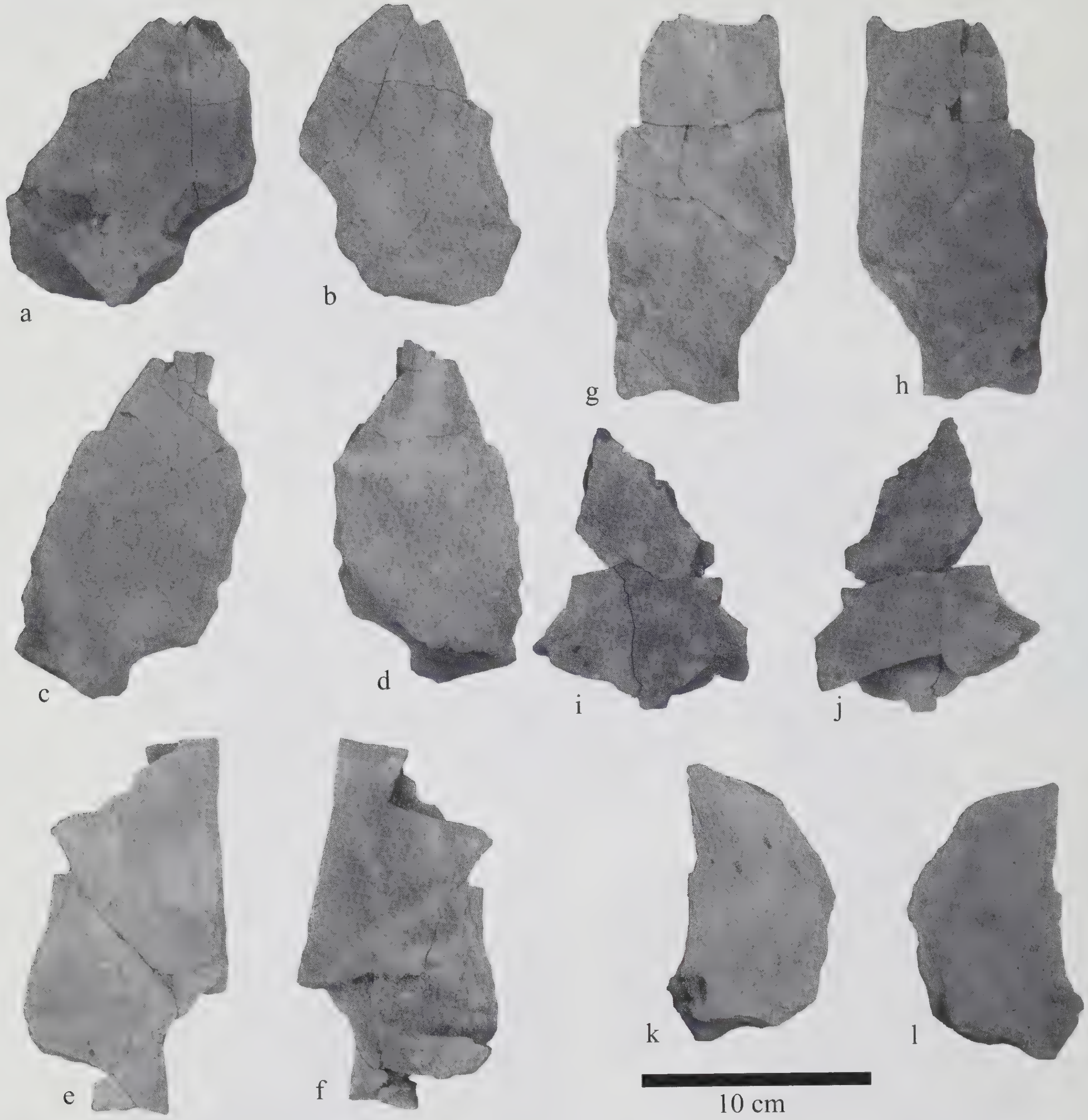

Figure 27.– *Squalodon whitmorei*, sp. nov., holotype isolated neural spines, USNM 183023. a-b, neural spine "A". a, left lateral view; b, right lateral view. c-d, neural spine "B" c, left lateral view; d, right lateral view. e-f, neural spine "C". e, left lateral view; f, right lateral. g-h, neural spine "D". g, left lateral; h, right lateral. i-j, neural spine "E". i, left lateral view; j, right lateral view. k-l, neural spine "F". k, left lateral view; l, right lateral view. Scale = 10 cm.

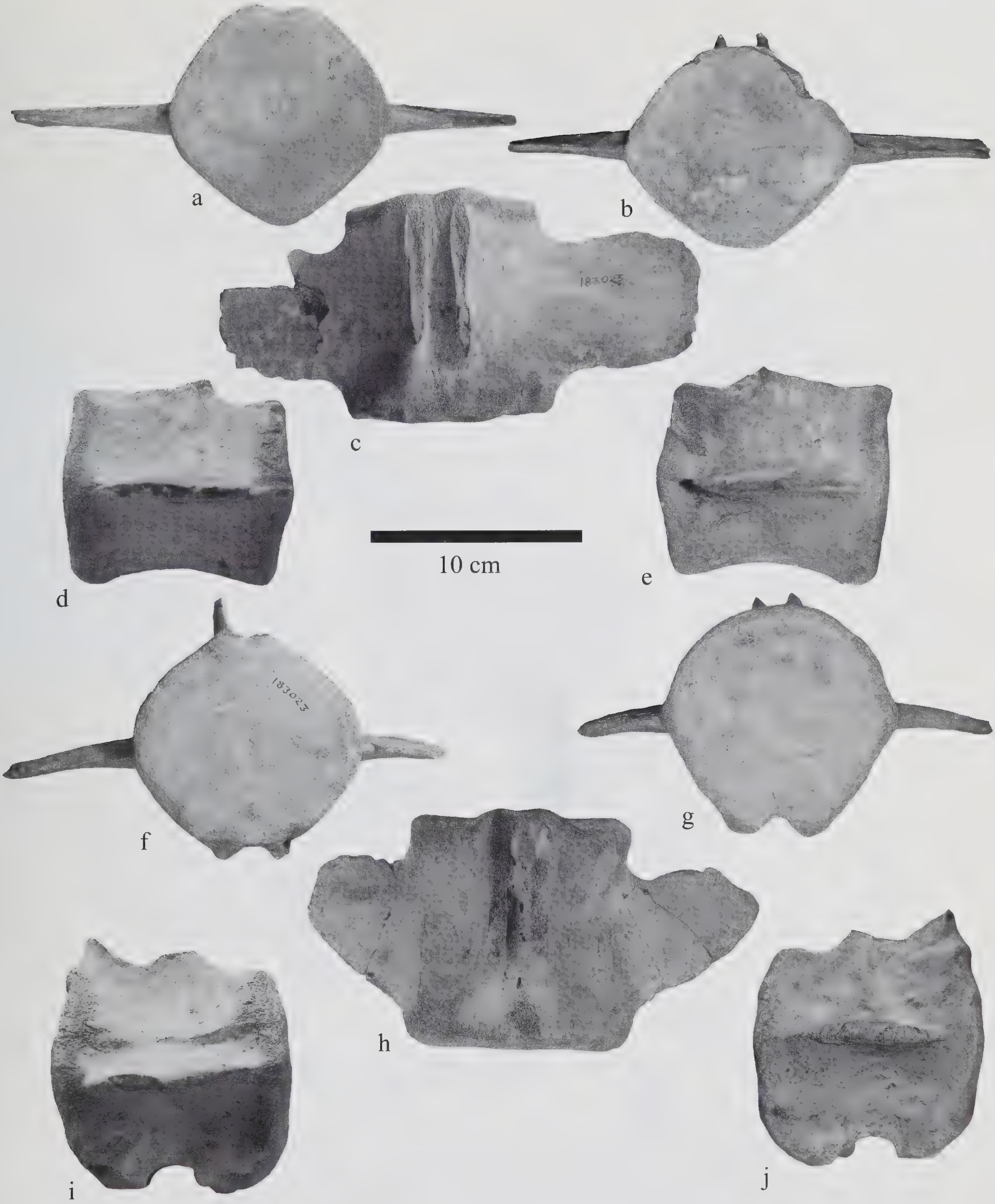

Figure 28.– *Squalodon whitmorei*, sp. nov., holotype caudal vertebra "1" and "2", USNM 183023. a-e, Ca"1". a, anterior view; b, posterior view; c, dorsal view; d, left lateral view; e, right lateral view. f-j, Ca"2". f, anterior view; g, posterior view; h, dorsal view; i, left lateral view; j, right lateral view. Scale = 10 cm.

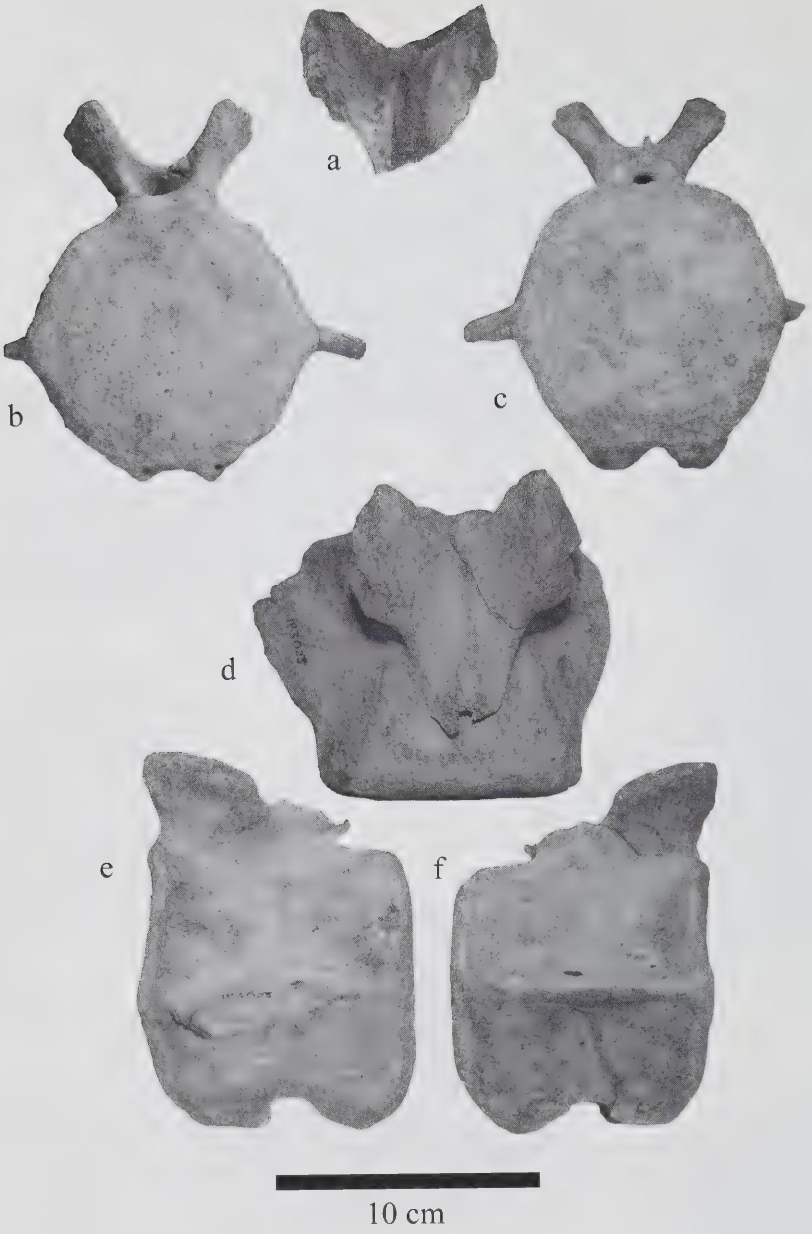

Figure 29.– *Squalodon whitmorei*, sp. nov., holotype caudal vertebrae “3” and “4”, USNM 183023. a, Ca”3”, dorsal view. b-f, Ca“4”. b, anterior view; c, posterior view; d, dorsal view; e, left lateral view; f, right lateral view. Scale = 10 cm.

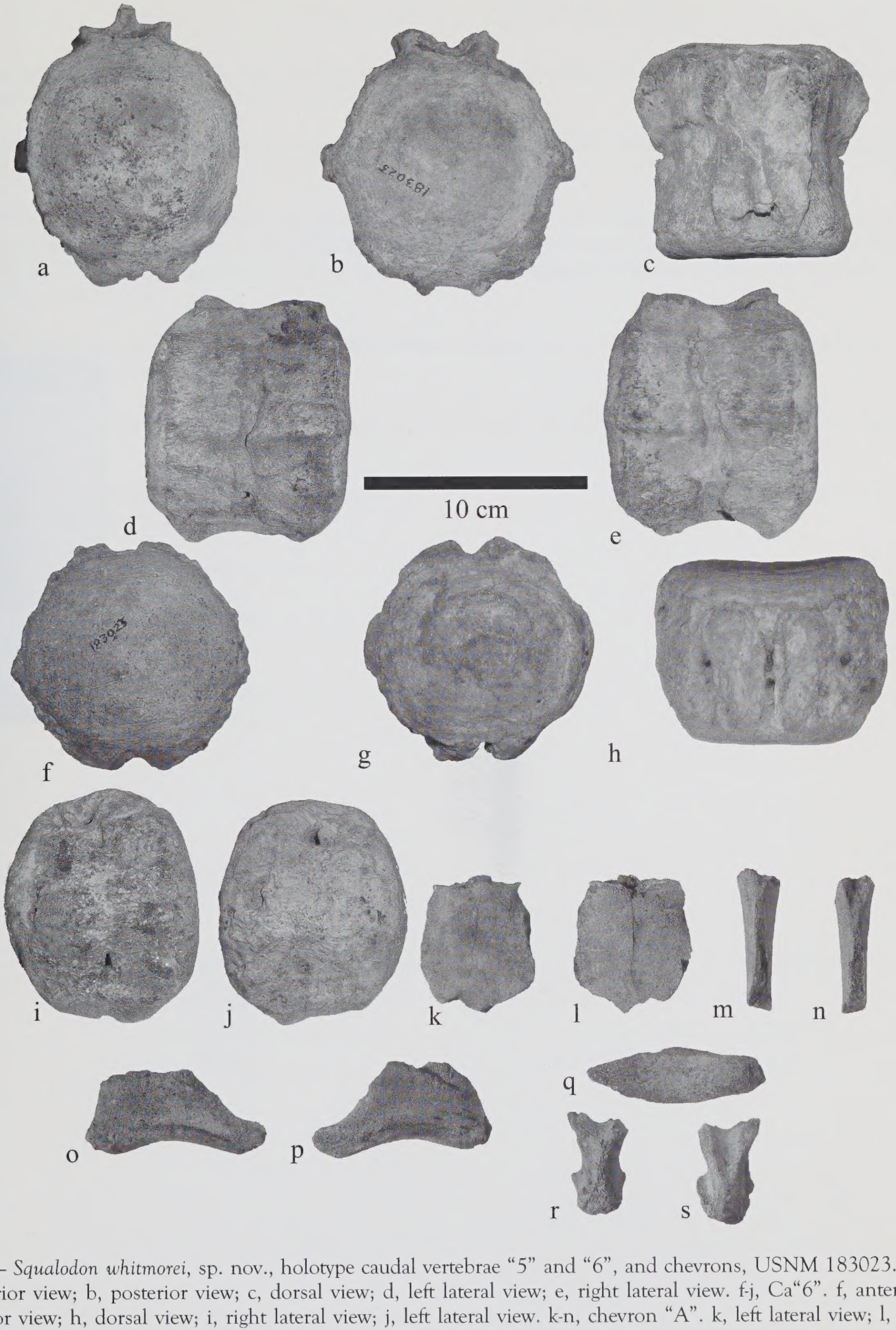

Figure 30.– *Squalodon whitmorei*, sp. nov., holotype caudal vertebrae "5" and "6", and chevrons, USNM 183023. a-e, Ca"5". a, anterior view; b, posterior view; c, dorsal view; d, left lateral view; e, right lateral view. f-j, Ca"6". f, anterior view; g, posterior view; h, dorsal view; i, right lateral view; j, left lateral view. k-n, chevron "A". k, left lateral view; l, right lateral view; m, anterior view; n, posterior view. o-s, chevron "B". o, left lateral view; p, right lateral view; q, ventral view; r, anterior view; s, posterior view.

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